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POULTRY BREEDING

POULTRY SCIENCE SERIES

EDITED BY

JAMES E. RICE

PROFESSOR EMERITUS OF POULTRY HUSBANDRY
NEW YORK STATE COLLEGE OF AGRICULTURE,
CORNELL UNIVERSITY

Poultry Breeding

BY MORLEY A. JULL, Ph.D., Professor and Chairman of Poultry Husbandry, The University of Maryland. Second Edition. Cloth; 6 by 9 inches; 484 pages; 76 figures.

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BY

MORLEY A. JULL

University of Maryland
College Park, Maryland

SECOND EDITION

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PREFACE TO THE SECOND EDITION

A REVIEW of the voluminous research in poultry genetics and allied fields conducted during recent years has resulted in an enlargement of the first edition of *Poultry Breeding*. The discussion has been brought up to date and in many respects is presented in more comprehensive form.

Chapter IX of the first edition, "The Inheritance of Linked Characters," has been made a part of Chapter III of the second edition, "The Mechanism of Inheritance." Chapters XI and XII of the first edition have been omitted from the second edition, except that much of the material in these two chapters has been incorporated in other chapters of the second edition.

The author is deeply indebted to Dr. T. C. Byerly, University of Maryland, for reviewing Chapters II and VI, and to Dr. C. W. Knox, United States Department of Agriculture, for reviewing Chapters III, VII, and VIII. Both have made valuable suggestions in connection with the manuscript for these chapters.

M. A. J.

COLLEGE PARK, MARYLAND
June 1, 1940

PREFACE TO THE FIRST EDITION

In many respects the greatest need of the poultry industry of every country is better-bred stock. Improvement in methods of rearing, feeding, and general management would accomplish much toward increasing the returns from the average flock of the country, but beyond a certain point further progress is impossible without an improvement in the breeding quality of the flocks. Since the numerous characters which the domestic fowl possesses are inherited, including color of plumage and ability to lay, and since many of the heritable characters are of economic importance, poultrymen everywhere should be as well informed as possible concerning principles and practices of poultry breeding in order that their work may be both interesting and remunerative.

The purpose of this book is to convey to its readers some conception of the manner in which various characters possessed by the domestic fowl are inherited. The discussion of fundamental principles involved should stimulate further research concerning the problems raised. The results of various lines of research work are reviewed and an extensive list of literature references is given, so that the investigator, teacher, and student each has a ready reference for review purposes.

The discussion of breeding practices to be followed should be of considerable value to extension workers, farmers, and commercial poultrymen. Moreover, since the most successful practices in breeding are based upon the fundamental principles of inheritance, it is obvious that every poultry breeder should know something of these principles in order to make his flock most successful from a practical standpoint. The value of progeny testing is made clear, for it is only by progeny testing that a breeder can expect to make the greatest progress.

A "Foreword" has been very kindly contributed by Dr. R. C. Punnett, of Cambridge University, where it was first determined that numerous characters of the domestic fowl are inherited along Mendelian lines.

The author is deeply indebted to the following authorities for reading and offering valuable suggestions in connection with the manuscript of the chapters accredited to each name: Chapter II, Dr. F. B.

Hutt, Minnesota Agricultural Experiment Station; Chapters III and VII, Dr. D. C. Warren, Kansas Agricultural Experiment Station; Chapter IV, Dr. L. C. Dunn, Columbia University; Chapter V, Dr. Walter Landauer, Storrs Agricultural Experiment Station; Chapter VI, Dr. T. C. Byerly, Bureau of Animal Industry, U. S. Department of Agriculture; Chapters IV, VIII, and X, Dr. C. W. Knox, Bureau of Animal Industry, U. S. Department of Agriculture; Chapter IX, Dr. F. A. Hays, Massachusetts Agricultural Experiment Station; the section on inbreeding and outbreeding in Chapter X, Dr. Lewis W. Taylor, California Agricultural Experiment Station. In addition, the entire manuscript was read critically by Dr. H. C. McPhee, Senior Geneticist, Bureau of Animal Industry, U. S. Department of Agriculture, to whom many thanks are due for numerous constructive suggestions.

The preparation of the book has been inspired by the hope of rendering the greatest possible service to the poultry industry.

M. A. J.

Washington, D. C.
June 1, 1932

FOREWORD TO FIRST EDITION

BY

R. C. PUNNETT

AGRICULTURE, most basic of industries, whereby man wrings his pittance from the soil, has of late years suffered much progress. And what is true of agriculture in general is true also of poultry in particular. To realize the nature of the change one has but to compare this book of Dr. Jull's with any of the standard works on poultry published ten or a dozen years ago. In taking advantage of his kind suggestion that I should write a foreword to the present volume, I do not think I could make better use of the pages at my disposal than to indulge in a few reminiscences and reflections on the way in which this change has come about.

Now in the industry there are three main things—rearing, feeding, and breeding; and the greatest of these is breeding. By rearing I include all those processes which start with the fertilized egg and end with the adult fowl. Industrially the most important of these has been artificial incubation; and the year in which Hearson first put on the market a really trustworthy self-regulating incubator must ever be a landmark for the rearer of poultry. Only then did it become possible for the industry to take advantage of the immense natural fecundity of the domestic hen. A minor invention, though very important, was that of the trap-nest at the end of last century, offering a simple and reliable method of isolating the best layers among a flock of hens. Among later developments, of which the ultimate outcome still hangs in the balance, must be mentioned the battery brooder and the use of electric light. All these things are contributions from the engineer. They are all appliances, enabling man to get more out of the hen, though without in any way altering her intrinsic qualities.

Feeding, again, is also a method of exploiting the hen without alteration in her intrinsic qualities. Great progress in this subject has been made in recent years, and we now know something about the rations necessary to keep the fowl in health and at the same time to get the utmost out of her in the way of production. The discovery of vitamins too has had its repercussions in the poultry-yard. Impor-

tant, however, as these things are—and they may spell all the difference between commercial failure and success—they go no further than enabling us to make the most of such hens as we may have. Neither the most scientifically balanced rations, nor the most discriminating dosages of vitamins will make a good layer out of a hen unless she possesses those natural qualities upon which productivity depends. A naturally good layer may do well even under adverse circumstances, but a naturally poor one will never do much though she be given the best of everything. And this is where breeding comes in, the knowledge of the transmissible qualities of poultry which enable us to build up and to maintain the ideal type of hen. This knowledge, as Dr. Jull explains in his third chapter, became possible only with the dramatic rediscovery of Mendel's classic paper on heredity in peas.

Now it was a fortunate thing for the poultry people, little as they probably realize it, that the moment of the rediscovery of Mendel's paper found William Bateson busy in Cambridge with a series of experiments on poultry.[1] He had started them with no idea of future commercial application. Like Mendel himself he chose his experimental material because it was convenient. He wanted to know how definite racial characters behaved on crossing, and so began the gathering of that knowledge which the industry is now turning to so good account. When he started there was all to know, and he began by working out the inheritance of such comparatively simple things as comb shape, and white plumage as opposed to colored. But simple as these things eventually turned out to be they seemed complex enough at first.

When I joined him in the work in January, 1904, it was still a puzzle why the walnut combs which came from crossing rose comb with pea comb should, when bred together, give single combs as well as the other three forms. There were those who clamored "ancestry," but Bateson's intellectual make-up was not of a kind to suffer mysticism gladly. So we went on breeding fowls for the sake of their combs, and out of it all eventually emerged the doctrine of the interaction of factors, one of the most important additions made to Mendel's original principles.

Another of the earlier experiments concerned the inheritance of white plumage. Early in his work Bateson had found both whites which were dominant to color and whites which were recessive. As the result of a long series of experiments involving White Leghorns,

[1] Bateson's notebooks, from the beginning of his experiments in 1898, are at present in my possession.

Dorkings, Rose Comb Bantams, Wyandottes and Silkies it was found that there were certainly three distinct types of white plumage, differing in their behaviour on crossing though all seemingly alike to the eye. It was an impressive sermon on the text that the plumage does not always proclaim the bird. And out of it all came the explanation of the curious phenomenon of "reversion on crossing," which to Darwin and many less wise heads had long been such a puzzle.

From the point of view of the poultry industry, 1905 was an important year in these experiments, for in that year we introduced the Silky fowl into our pens. Our original intention had been to study the relations of the peculiar comb of this breed, and for this purpose it was reciprocally crossed with the Brown Leghorn. The result was something new and unexpected. For whereas the light skin of the Leghorn was dominant in both sexes when Silky hen was mated with Leghorn cock, the reverse cross gave also cocks with light skins but hens with *dark* ones. The point about the combs was thrust aside, and our attention was entirely given to this new phenomenon, the like of which Leonard Doncaster was also finding in his experiments with the currant moth. The clue was suggested by some experiments with sweet peas which we were making at the same time, and the outcome was the formulation of the principle of sex-linkage in 1908.[2] But although formulated so many years ago some time was to elapse before it became of practical importance to the industry.

In 1909 Bateson left Cambridge to take up the directorship of the John Innes Horticultural Institution just founded at Merton, and thenceforth his interests were mainly botanical. But during those years at Cambridge he had laid the foundations of the study of heredity in fowls. The inheritance of many characters such as comb shape, shank color, plumage color, etc., had been definitely worked out, and the knowledge made available to the breeder, did he choose to make use of it. But the main achievement was the demonstration that such various characters in poultry are all subject to the same general scheme of heredity to which Mendel first provided the clue. Far as we were from complete knowledge, the Cambridge experiments showed that such knowledge was to be had, and showed further the method to be pursued.

Moreover, the work had been done in the face of difficulties which experimenters in these days of endowed research probably do not

[2] How Bateson hit upon this is vividly told in a letter of his dated January 9, 1908, to be found in "William Bateson, His Essays and Addresses," Cambridge University Press, 1928, p. 113.

realize. It was all a private venture in a little paddock at the back of Bateson's house, aided by such precarious and trifling sums as could be coaxed out of sundry societies from the meagre grants at their disposal. For at the time this kind of work was little in favor in scientific circles; and biologists, such as were not actively hostile, were as a whole more or less indifferent.

However, what Bateson achieved before leaving Cambridge had begun to turn the scale, and in 1911 the then Board of Agriculture set aside a small annual grant in aid of the experiments which I continued to carry on in Cambridge. I was then joined by P. G. Bailey, who was so soon to lose his life in the war, and we started experiments on certain characters showing what was then called "blended inheritance." For at that time it was held by many that such inheritance was of a different type from Mendelian heredity with its clear-cut ratios. As examples we chose body weight and egg color, and we were able to demonstrate, to our own satisfaction at any rate, that, although such cases are more complicated, they are none the less capable of interpretation in terms of relatively few definite Mendelian factors.

Our experiments on body weight, starting with Hamburghs and Sebright bantams, were also designed to test the heredity of henny plumage, and of silver and gold. We paid special attention to the down colors of our chicks, and in proving that silver and gold form a sex-linked pair we were at the same time able to correlate these colors with the down characters. We also showed that barred and black were likewise betokened in the down at hatching. Even then the matter remained for us one of purely scientific interest, and it was only by chance, when reading some correspondence at the Food Production Department during the war, that it occurred to me that the knowledge could be of commercial value. This was pointed out in a brief article in the Journal of the Board of Agriculture for February, 1919, and although it was some years before the idea was entertained seriously it eventually made its way. Today millions of chicks are reared annually from sex-linked crosses in this country,[3] and although America is rather more backward, I have little doubt that the advantages of the method will soon make an equal appeal there also.

More recently an interesting development has taken place in connection with sex-linkage. About ten years ago Mr. M. S. Pease and I

[3] A well-known firm, which hatches annually about a million chicks, in 1929 put into their incubators about 30,000 eggs produced from sex-linked crosses. In the present year (1932) they have made arrangements to put in over 800,000

started some experiments on the inheritance of the transverse barring on the feathers of fowls. We knew that the barring of the Plymouth Rock was dominant to self-color and sex-linked; we knew also that the barring of the Hamburgh and the Campine was recessive to self-color and not sex-linked. How were these two types of barring going to behave when present simultaneously? We thought that a knowledge of their combined effect might possibly shed some light upon the rhythm of feather growth, so we built up a strain which was pure for the two types of barring. And when we made it we found that the downs of the chicks were quite different in the two sexes, in spite of the fact that the strain bred perfectly true to plumage characters. We had made a breed that automatically sex-linked itself. At present it is being worked up for increased productivity. When this has been done, and the "Cambar" is loosed on the world in a few years' time, it should prove acceptable and profitable to those who wish to make use of the sex-linked result without the operation of crossing.

Even more recently a further development has taken place in connection with ducks. The Indian Runner duck, and its derivative the Khaki Campbell, are the finest egg machines in the world. But for table purposes the drakes are relatively worthless. Two years ago we succeeded in our quest for a sex-linked down character in ducks, and today we are engaged in building up breeds of Runners and Campbells giving a clear-cut sex-linked down character. This will enable the breeder to get rid of the worthless drakes at hatching, and should provide a definite stimulus to the increased production of these magnificent layers.

Such is a brief sketch of some of the poultry work at Cambridge since Bateson opened his first notebook in 1898. Materially it has greatly profited humanity, for when sex-linkage has entered fully into the procedure of the industry the world will be millions a year the richer for this one discovery alone. But it is not upon this aspect of the work that I wish to insist, for it is the moral to be drawn from it all that seems to me to be of by far the greater value. We have before us one of the most striking applications of scientific discovery to a great industry, and it is worth reflecting for a moment on the manner in which it has come about.

In these days we hear much of "team work" and of "organized research," but in the experiments I have written of that is all to seek. The span of time sketched out is 33 years, and during more than a third of these there was but a solitary worker in charge. Nor were the means provided ever on a lavish scale. In earlier days we had to do much of the menial labor ourselves; and though of late

years the means have been sufficiently ample I should be much surprised if, over the whole period, the expenditure on upkeep and labor averaged as much as $2,000 a year. That so much was done with so little was of course due to William Bateson. He led and others followed.

It needs the big man to get the big thing done, and therein lies the lesson for the industry. Its problems are many and vital, and I doubt if they are going to be solved by any number of teams of second-raters, however numerous and well endowed. Rather would I suggest the policy of buying a few of the very best of the younger intellects, picking them from among the physiologists, the biochemists and the geneticists. It is all to the good that they should come to the job with fresh minds, innocent of fowl. To such men I would pay whatever was asked, and ungrudgingly bestow upon them all the hewers of wood and drawers of water they demanded. Discovery is a gamble and quite beyond the power of the wisest to control. But if one in ten succeeded the plan would have worked reasonably well.

As I see it today the greatest need of the poultry industry is fine intellects. They are rare, and must therefore be paid for; but in the long run it is worth it. Huxley once said that a potential Faraday would be cheap at a quarter of a million pounds sterling. He would indeed. But the finest constructive brains are reasonably modest in their requirements so long as they think they are being treated fairly. And since they have a way of relying on their intellect rather than their material equipment they are very much cheaper to run. However, I have labored the point enough, for I do not suppose that it will ever be acted upon. Special privileges in a democracy are reserved for champion boxers, film stars and multimillionaires.

There remains but one last reflection that I shall allow myself to make. No one who reads intelligently this book of Dr. Jull's can allow his thoughts to stay at the hen. He cannot but feel that what is written here is only part of some great scheme into which all of us living creatures must willy-nilly fit. It is true that we know far more of heredity in the fowl than in man. Since Mendel was rediscovered more than thirty generations of hens have passed, which for man would mean a thousand years in the sight of the geneticist. There can be little doubt that much of what is here recorded concerning the nature of the hen offers the clue to much that is puzzling in ourselves. It is not in Dr. Jull's province to write of man, interesting creature though he be; those who wish to follow up this track of thought cannot do better than read the volume of Bateson's "Essays" already referred to above. But let him not do so if he fear to discover that of him also is the story told.

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POULTRY BREEDING

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CHAPTER I

BREEDS AND VARIETIES AND THEIR SIGNIFICANCE

The numerous existing breeds and varieties of domestic fowls, with plumage colorations and structural features in great variety, have been developed by breeding methods practiced by man throughout the ages. Because of their relatively small size as compared with many other domestic animals and because of their adaptability to a wide variety of climatic conditions, fowls have entered into the interests of more human beings than any other animal. For thousands of years and in all parts of the world the domestic fowl has been bred by all classes of mankind.

From rather limited beginnings, the original wild fowls of the bamboo jungles of India have been developed into stocks noted for their fighting propensities or for their beauty of form and plumage pattern or for their excellence as table fowl or for abundant egg production. The relatively primitive wild type has been developed into different breeds and varieties with diverse characters adapted to different purposes, some purely aesthetic and some largely utilitarian.

The Origin of the Chicken. The most authentic information available regarding the origin of the chicken indicates that all the breeds existing today have descended from one or possibly four subspecies of wild fowl. The four subspecies are as follows:

1. *Gallus gallus* or *Gallus bankiva*, the Red Junglefowl.
2. *Gallus lafayette*, the Ceylon Junglefowl.
3. *Gallus sonnerati*, the Gray Junglefowl.
4. *Gallus varius*, the Javan Junglefowl.

The Javan Junglefowl differs from the other three species in having a single-median wattle, a smooth-edged comb, truncated neck hackles, and an extra pair of rectrices, or tail feathers.

The eminent naturalist Darwin (1868)[1] who made a close study of the origin of the domestic fowl, concluded that all our domestic stocks descended from one species, the Red Junglefowl. The principal reason why Darwin regarded the Red Junglefowl as the progenitor of all our

[1] A list of the literature references cited in each chapter is given at the end of the chapter.

domestic breeds of poultry was that he observed that it resembled some of the early domestic breeds more closely than the other three species; its voice was more similar to the voice of the domestic fowl; and when mated with domestic stock it produced offspring more freely, and the offspring were much more apt to be fertile than hybrid offspring from any of the other species.

Houwink (1911), as the result of extensive observations, was inclined to agree with Darwin's viewpoint; but in later years, as a result of breeding experiments, he came to believe that our domestic breeds have not descended from the Red Junglefowl only.

Beebe (1918–1922) states that all four subspecies will cross with one another and that the hybrids are more or less fertile among themselves. Many references are cited where crossing has taken place among the four wild species and domestic stocks. The matings sometimes occurred naturally and sometimes the natives of India and Java encouraged crossing. In his exhaustive study of the wild fowl, Beebe states definitely, "There is no doubt that the Red Junglefowl alone is the direct ancestor of all of our domestic poultry, so this question is removed from the discussion."

On the other hand, Tegetmeier (1873), a co-worker with Darwin, finally arrived at a different conclusion from that of Darwin concerning the origin of all our domestic fowl. Tegetmeier pointed out that numerous hybrids were obtained from crossings between domestic stocks and the Ceylon and Javan Junglefowls. He further held: "I have no doubt in my own mind that the wild *Galli* have intermixed in not a few instances, and perhaps through not a few centuries, in producing our domestic breeds." Tegetmeier was especially doubtful of the Asiatic races of domestic fowl, Brahma, Cochin, and Langshan, being derived from the Red Junglefowl. In these three breeds the long axis of the opening of the skull through which passes the spinal cord is perpendicular, whereas in the four subspecies of Junglefowl and in practically all domestic breeds except the three Asiatic breeds mentioned the opening is horizontal.

Fertile offspring between the Gray Junglefowl and domestic fowls have been raised by Ghigi (1916), and he is led to believe (1922) that some of the domestic breeds are descended from a wild species now extinct. Lotsy and Kuipper (1922, 1923, 1924) conducted experiments in crossing representatives of the four wild subspecies with domestic stocks, the results of which give added evidence to the production of fertile hybrids in all the matings. The results secured by Houwink, as reported by Lotsy and Kuipper, give added evidence to the claim that our domestic breeds are not descended from *Gallus bankiva* only.

Furthermore, Punnett (1923) refers to a second-generation hybrid bird from a cross between the Red Junglefowl and the Javan Junglefowl, the hybrid being black in color. Regarding the significance of the appearance of this black hybrid, Punnett makes the interesting observation that the Javan Junglefowl may be one of the ancestors of some of our domestic breeds.

From the results secured from reciprocal matings between each of the four subspecies of Junglefowl and the domestic fowl, Hertwig (1936) concluded that the ancestors of the domestic fowl included the four Junglefowl subspecies, since fertile offspring were obtained from all matings except the female progeny of the mating of the Javan Junglefowl male and the domestic female.

In conclusion, it must be admitted that not until representatives of the four wild species can be obtained that are known to be pure, and proper crosses are made among them and with domestic stocks, can the problem of the origin of domestic breeds be definitely established.

Early Influence of Cockfighting. That the sport of cockfighting exercised a tremendous influence not only in the domestication of wild birds but also in the subsequent distribution of the fowl is amply demonstrated by the importance attached to the pastime by many human races. The literature of various nations contains many references to the sport, and Brown (1929), who has given much thought to the question, concluded that the sport of cockfighting had as much responsibility for the domestication of the fowl as demand for food, and that the sport was chiefly instrumental in making the species popular.

Influence of Exhibitions. With the suppression of cockfighting as a public institution, poultry exhibits had their inception. In 1849 the first poultry show was held in America at Boston, and about the same time the first poultry show was held in England. These exhibitions gave impetus to the growing interest in the then known breeds and varieties of fowl, for, by that time, several countries had each developed races possessing characters differentiating them from races produced in other countries. India had produced its fighting cocks, Asia its massive breeds with feathered shanks, Italy its small-bodied birds with nervous dispositions, England its gamecocks and breeds excelling in fleshing properties, and America its numerous early breeds.

Poultry exhibitions had the effect of encouraging breeders to pay considerable attention to such characters as type, color markings and pattern, and other characters that were soon adopted as standard for the breed and variety in question. This has often been carried to extremes, to such an extent that the vigor and economic qualities have

sometimes been sacrificed in the perfection of some character of minor importance.

Poultry exhibitions tended to encourage the development of new breeds and varieties. This was especially true of breeds and varieties with what are often called "fancy" characteristics. Consider, for instance, the miniature bantams, where smallness of size is one of the outstanding features. Consider also the vulture hocks on the Sultan breed, the highly developed crest on the Polish breed, the peculiar type of the Pit and many other Games, and the bewildering variety of color patterns in a large number of varieties.

What Constitutes a Breed? As with other classes of livestock, so with the domestic fowl, the chief interests in breeding operations led to the establishment of breeds. Breeding for improvement was carried on largely from the standpoint of perpetuating desirable characteristics possessed by races or strains. In other cases new breeds were developed by crossing existing breeds and then practicing rigid selection until the desired characters were transmitted with reasonable regularity.

The distinguishing feature whereby one breed of fowls differs from another breed is the "type," although this is rather confusing since the visible body type is influenced not only by the actual shape of the body but also by the feather contour. In breeding standardbred poultry, the type of a bird as determined by feather contour has been regarded as of greatest importance, so much so that in many cases the actual body type has received minor attention. The situation has developed so that it is now recognized that "shape makes the breed," shape here indicating very largely feather contour.

A breed represents a group of domestic fowls in which is inherited from generation to generation a distinctive shape of body as exemplified largely by plumage contour. Other characteristics such as shape of comb, color of earlobe, color of egg shell, and number of toes are possessed by all birds belonging to any one breed but are characteristics common to each of several breeds.

Varieties Within the Breed. Within each breed of fowls there naturally was a tendency to segregate various color combinations or, where only one color existed in the original breed, to develop new color patterns. In either case, it was necessary to adhere to the original type or shape characteristic of the breed, and thus it has arisen that varieties of a breed are supposed to be identical in all characteristics except plumage color or, in some cases, shape of comb, standard weight, color of shanks, and other minor characteristics. There is a large grain of truth in the old saying of poultry breeders that "shape makes the breed and color the variety."

Breed and Variety Descriptions. Detailed descriptions of the different breeds and varieties are contained in numerous "standards" published by specialty clubs and breeders' organizations. In many cases the ideal specimen of the breed or variety is illustrated; in the United States and Canada, for instance, the "Standard of Perfection" (1938) serves as a guide in determining the relative merits of birds shown at exhibitions and used in breeding pens. The American Standard of Perfection, however, contains descriptions and illustrations of breeds recognized by the American Poultry Association, and for descriptions of other breeds reference should be made to club books published by the specialty breeding clubs in various countries.

In order to simplify the description of the numerous breeds and varieties being bred in different countries, several characters, such as type of comb, color of earlobe, skin, and shanks, shank-feathering or its absence, color of egg, and the standard weights of the cock, hen, cockerel, and pullet, are given in tabular form in Tables 1 and 2. The inheritance of a number of these characters is discussed in subsequent chapters.

Since the particular interest in this book is a discussion of inheritance of the characters possessed by different breeds and varieties, and since those characters the inheritance of which has been investigated are discussed in subsequent chapters, it is necessary at this time only to make a few general observations regarding the outstanding differences that exist among breeds and varieties.

Mention has already been made of the fact that the members of each breed have a characteristic shape which really refers to the outline of a bird as determined by its feather contour. From this standpoint some breeds are distinctly different from others. The Leghorn has more pronounced curves than the Rhode Island Red. The Plymouth Rock has a longer and broader body than the Wyandotte. The Langshan is what might be termed "upstanding," with a sharply curved back, whereas the Cochin is "low-set," the back being short in appearance and that of the female having a pronounced "cushion." The Minorca has a rectangular-shaped body tilted downward from front to rear, whereas the Cornish is much broader over the shoulders than at the rear and the back is slightly convex. These are a few examples of differences in breed type.

On the other hand, there are different breeds that are very similar in type. The Leghorn and the Ancona are much alike in outline. The Orpington, Plymouth Rock, and Sussex have much the same shape of body. Other breeds also show similarity of outline as far as feather contour is concerned, minor differences being confined for the most

part to the carriage of the tail and the extent of feather development in certain other sections.

Stripped of their feathers, the bodies of many breeds are difficult to distinguish as far as shape is concerned. Dressed roasters of the Brahma, Jersey Grant, Orpington, Wyandotte, New Hampshire, Plymouth Rock, and Rhode Island Red breeds exhibit about the same proportions of the different parts of the body. Leghorn, Wyandotte, New Hampshire, and Plymouth Rock broilers are sometimes difficult to distinguish, especially if the heads and legs are concealed or are severed from the body. From the economic standpoint, therefore, it is apparent that feather contour bears no relationship to flesh production.

From the standpoint of plumage color, the breeds and varieties may be divided into two groups: (1) breeds and varieties that are of one color and are called solid-colored or self-colored; (2) breeds and varieties that are of two or more colors and are called parti-colored.

The self-colored group includes whites, blacks, blues, reds, and possibly buffs, although buffs frequently carry some black. The parti-colored group includes breeds and varieties that have, among others, the following kinds of plumage: barred, black-red, mottled, pied, pyle, spangled, columbian, silver-laced and golden-laced, and silver-penciled and golden-penciled.

A description of the plumage of breeds and varieties is simplified because the parti-colored plumage pattern of some varieties belonging to different breeds is identical. The Dark Brahma, Silver-Penciled Plymouth Rock, and Silver-Penciled Wyandotte have the same plumage pattern; so also have the Partridge Cochin, Partridge Plymouth Rock, and Partridge Wyandotte, and likewise the Light Brahma, Columbian Plymouth Rock, and Columbian Wyandotte.

The plumage pattern of a variety of one breed may appear distinctly different from that of a variety of another breed although the only difference is that silver or white in one replaces red or reddish bay in the other. For instance, this is the only difference between the plumage pattern of the Silver-Penciled Wyandotte and the Partridge Plymouth Rock, the male and female of each variety being shown in Fig. 1. It is apparent, therefore, that in developing the numerous varieties poultry breeders have made many crosses in order to combine plumage pattern and breed type.

Then, again, in several breeds there are two varieties in which a single difference makes the varieties appear quite distinct. The Partridge Plymouth Rock is similar to the Silver-Penciled Plymouth

Rock except for the single difference that the "silver" or white of the latter variety replaces the "gold" or red or reddish bay of the former. The single difference between the Golden-Laced Wyandotte and the Silver-Laced Wyandotte is that the "silver" or white of the latter

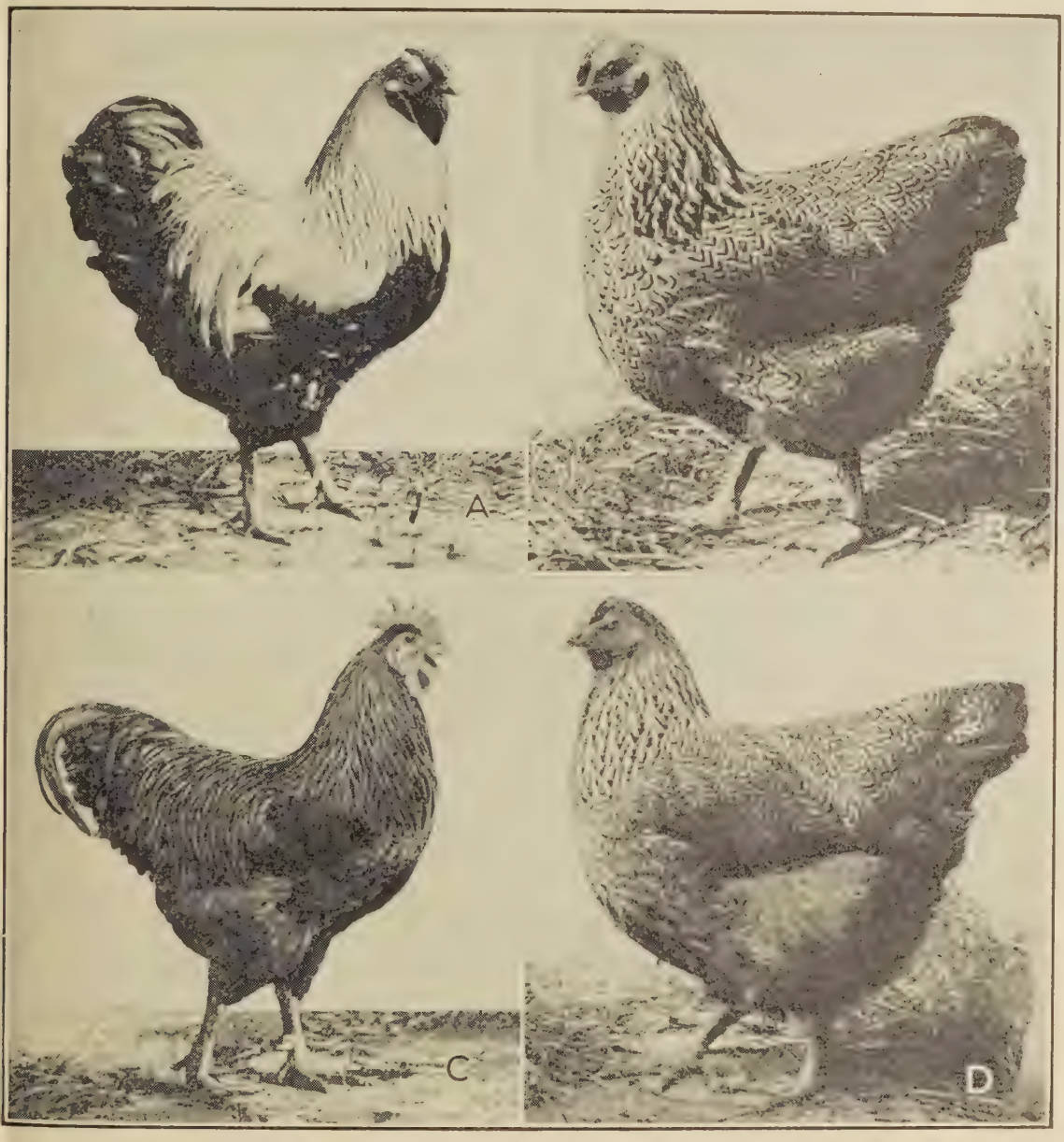

FIG. 1. As far as plumage color is concerned, the Silver-Penciled Wyandotte, shown above, differs from the Partridge Plymouth Rock, shown below, in that white replaces golden bay. The plumage pattern in the two males is identical and the same is true in the case of the two females. (U. S. D. A.)

replaces the "gold" or golden bay of the former. The same is true of the Golden Campine and the Silver Campine, and of certain varieties in other breeds.

White Plumage. Among the various white breeds may be mentioned the Chantecler, Rhode Island White, and White-Booted Bantam. A white variety is to be found in many of the different breeds, such as

Cochin, Leghorn, Minorca, Orpington, Plymouth Rock, Wyandotte, Silkie, and Rose-Comb Bantam.

Black Plumage. One of the most popular black breeds is the Jersey Black Giant, although there is a black variety in each of several breeds, including the Langshan, Leghorn, Minorca, Orpington, Wyandotte, and Rose-Comb Bantam. The Crevecoeur and La Fleche are two black breeds of French origin.

Buff Plumage. A buff variety is to be found in many of the breeds, such as Brahma, Cochin, Leghorn, Orpington, Plymouth Rock, and Wyandotte.

Blue Plumage. The Andalusian is the only blue breed, but there is a blue variety in each of the following breeds: Leghorn, Orpington, and Plymouth Rock.

Red Plumage. The Red Leghorn is one of the very few varieties that is solid red in plumage color.

Red and Black Plumage. There are several breeds and varieties in which the plumage colors are confined to a combination of red and black. The Rhode Island Reds belong to this group, the plumage being red over the body with black in the wings and tail. Red Sussex, New Hampshires, Black-Breasted Red Games, and Black-Tailed Red Leghorns also belong to this group.

Barred Plumage. There are three kinds of barred plumage: (1) alternating black and white bars, (2) alternating black and golden bay bars, (3) alternating white and golden bay bars.

Among the breeds having black and white barring are the Cambars, Dominiques, and Scotch Grays, and among the varieties having black and white barring are the Barred Plymouth Rocks, Cuckoo Leghorns, Silver Campines, and Silver-Penciled Hamburg females, which are in reality barred rather than penciled. It is interesting to note, as pointed out in Chapter IV, that the barring of the Barred Plymouth Rock behaves differently in inheritance from the barring in the Silver Campine and Silver-Penciled Hamburg.

The Golden Campine and Golden-Penciled Hamburg females are two varieties that have barring comprised of alternating bars of black and golden bay.

The Chamois Campine has alternating bars of white and golden bay.

Spangled Plumage. In the Silver-Spangled Hamburg the plumage is white except that each feather is tipped with a black spangle. In the Golden-Spangled Hamburg the plumage is golden bay except that each feather is tipped with a black spangle. In the Speckled Sussex the plumage is mahogany bay in color except that each feather

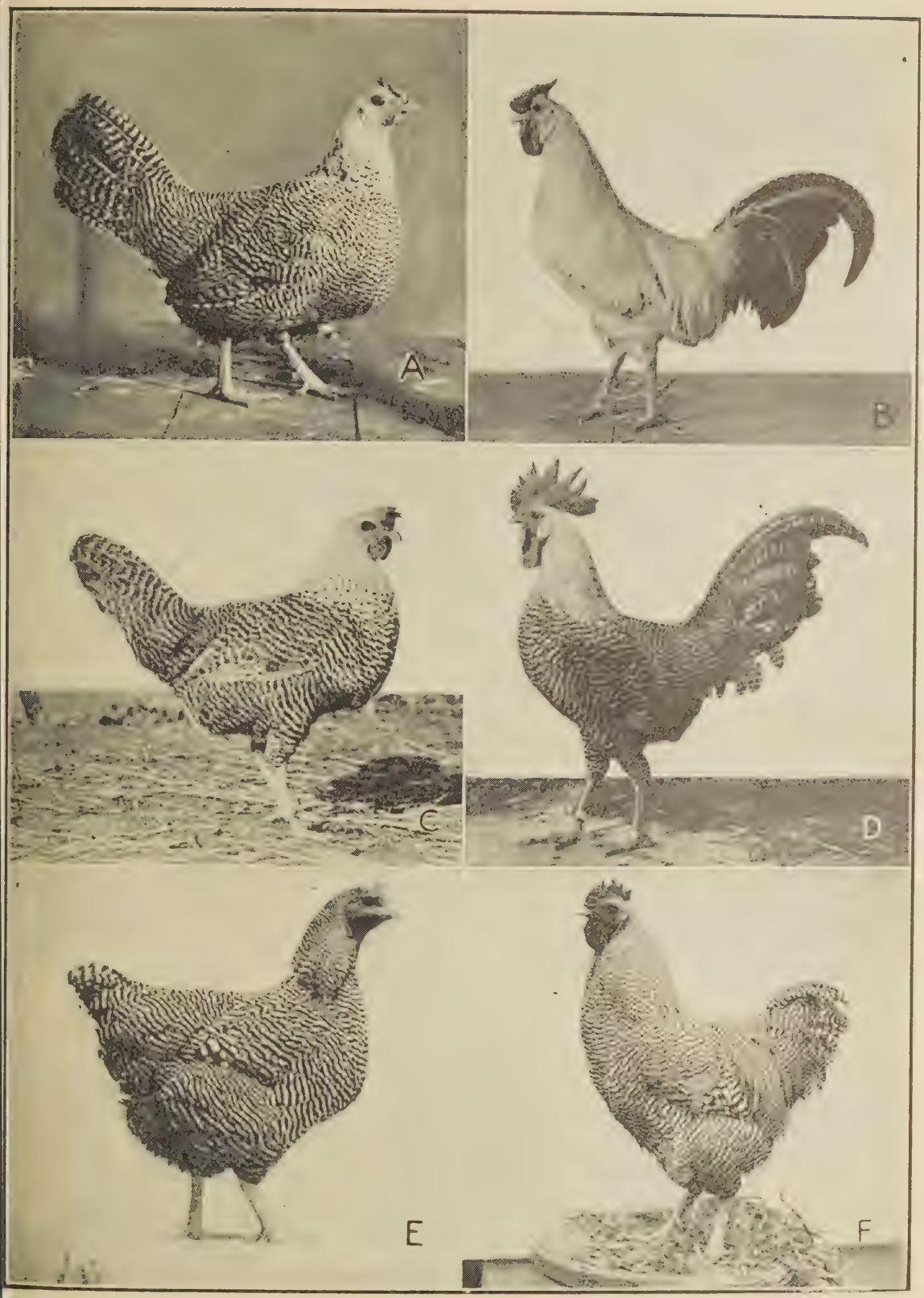

FIG. 2. Black-and-white barring in three different varieties. The Silver-Penciled Hamburg, shown at the top, is in reality a barred variety but in the male barred feathers are restricted to the wings and the sides of the body. In the Silver Campine, shown in the middle, the black bars are much wider than the white bars. In the Barred Plymouth Rock, shown at the bottom, the black and the white bars are supposed to be of equal width. The barring character in Barred Plymouth Rocks behaves differently in inheritance from the barring character in the other two varieties. (U. S. D. A.)

is tipped with a white spangle, a crescentic black bar dividing the white spangle from the mahogany bay. The Buttercup female for the most part has golden buff plumage with black markings, called spangles, diagonally across each feather.

Mottled Plumage. In the Ancona breed and the Mottled Houdan and Mottled Java varieties the plumage is black but a few of the feathers are tipped with white, giving a mottled effect.

Pied Plumage. The Exchequer Leghorn has plumage comprised of a mixture of black and white, which is called pied.

Pyle Plumage. A striking plumage coloration is seen in Red Pyle Games, the sexes differing in an outstanding manner. In the male the plumage on the head and at the back of the neck is orange colored; over the back and wing-bows it is red; the rest of the plumage, except for the wing-bays, is white. In the female the plumage is white over all parts of the body except that the head plumage is golden, the feathers on the front of the neck are white tinged with salmon, and the breast feathers are salmon.

Columbian Plumage. In Light Brahma, Columbian Plymouth Rock, Columbian Wyandotte, and Light Sussex the plumage is white except that the hackle and saddle feathers in the male and the neck and tail coverts in the female are black edged with white, the tail feathers in both sexes are black, and there is some black in the wings.

There are some breeds that exhibit certain modifications in the extension of black pigment as seen in the typical columbian plumage, as shown in Fig. 31. For instance, in the Black-Tailed Japanese Bantam, some of the wing and tail feathers are black but there is no black in the neck feathers. On the other hand, in a German breed called Lakenfelder the neck feathers are solid black, some of the wing feathers and the tail feathers in both sexes are black, and in the male the saddle feathers are also black. These two cases illustrate the extent to which minor variations in color pattern occur among the various breeds of domestic fowl. Among breeds whose plumage pattern comprises several colors the variations are more extensive although the ground color may be very similar.

Laced Plumage. A feather is said to be laced when the edge is of a different color from the rest of the feather. There are silver-laced breeds and varieties and golden-laced breeds and varieties, the only difference being that in the silver-laced breeds and varieties the neck feathers of the female and the hackle and saddle feathers of the male are black laced with white and the rest of the plumage in both sexes is white, most of the feathers being laced with black, whereas in the golden-laced breeds and varieties the neck feathers of the female

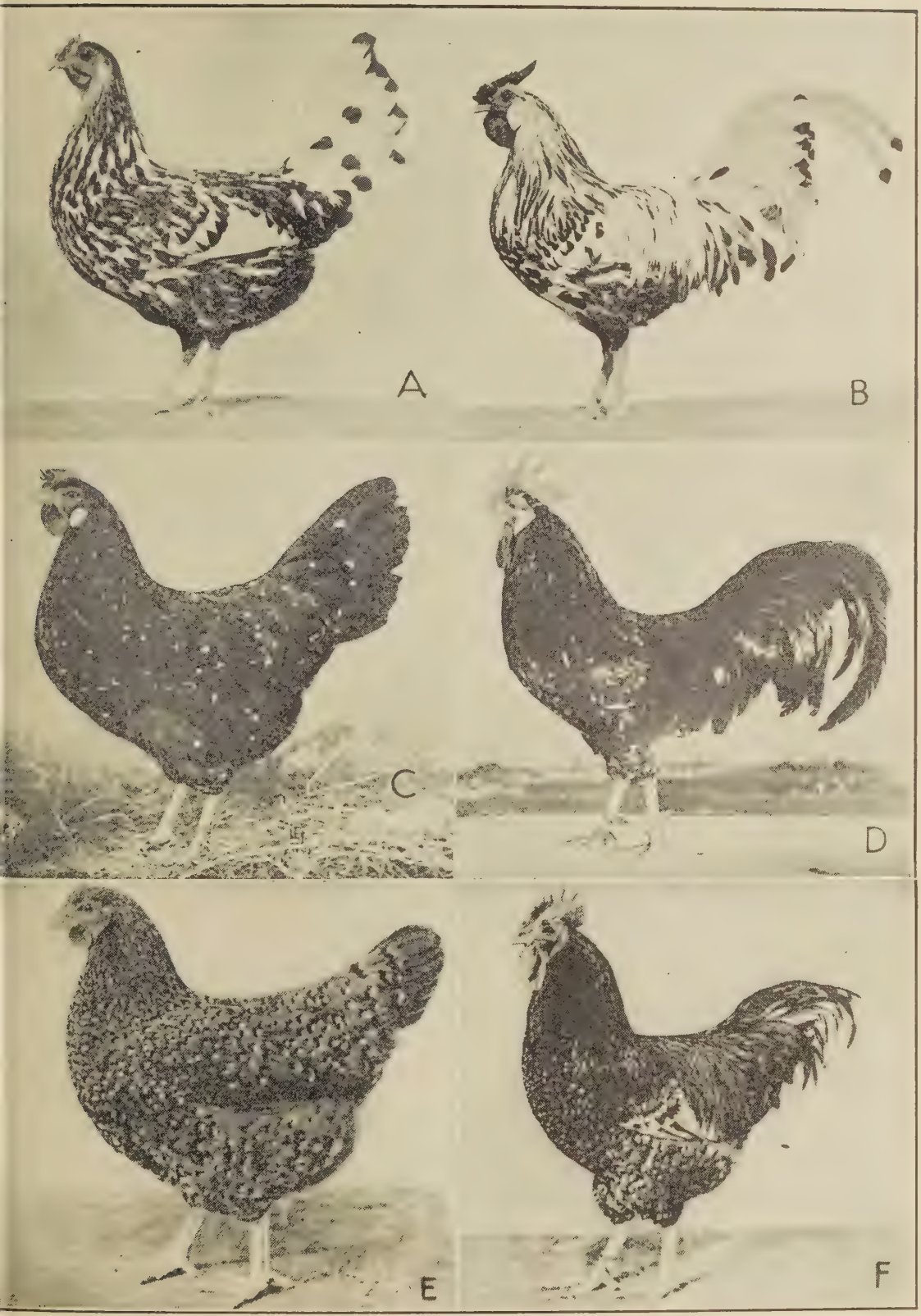

FIG. 3. Spangled plumage in the Silver-Spangled Hamburg, shown at the top; mottled plumage in the Ancona, shown in the middle; white tipping in the Speckled Sussex, shown at the bottom.

and the hackle and saddle feathers of the male are black laced with golden bay and the rest of the plumage in both sexes is black, most of the feathers being laced with golden bay.

White lacing on red feathers is found in White-Laced Red Cornish, and white lacing is also encountered in Buff-Laced Polish, the creamy white lacing being on golden buff feathers.

Blue lacing is encountered in Blue Andalusians and blue varieties of other breeds; in this case, however, the lacing is due to a difference in shade of blue.

Penciled Plumage. A feather is said to be penciled when there are crescentic markings of a different color from the rest of the feather, these crescentic markings being one, two, or three in number depending upon the breed or variety. Moreover, penciling is confined to the female of the brced or variety. In the Dark Cornish female the feathers over most parts of the body are bay in color and have a lacing of black together with one crescentic black penciling mark, whereas in the Dark Brahma female two or three black penciling marks appear on a white feather.

The white ground color in the Dark Brahma, Silver-Penciled Plymouth Rock, and Silver-Penciled Wyandotte female is replaced with reddish bay in the Partridge Cochin, Partridge Plymouth Rock, and Partridge Wyandotte female; otherwise their plumage pattern is identical.

Stippled Plumage. In the Light Brown Leghorn female the feathers over the back and sides are dark brown stippled with lighter brown, the stippling constituting numerous clearly defined specks in each feather. In the Dark Brown Leghorn female there is coarse reddish brown stippling in the black portion of each feather over the back and breast. In the Silver-Gray Dorking female all the plumage, except the neck feathers and the primaries and secondaries, is gray, each feather being finely stippled with silvery white. Stippling is also found in Silver Leghorn females and in females of some of the Game varieties, including the Black-Breasted Red, the Golden Duckwing, and the Silver Duckwing.

Majority of Breeds and Varieties Accounted For. The various colors of plumage that have been mentioned previously embrace the great majority of the more popular breeds and varieties. The breeds whose general plumage color has been mentioned include the Ancona, Andalusian, Australorp, Jersey Black Giant, Buttercup, Dominique, Rhode Island Red, Rhode Island White, Black Sumatra, White-Faced Black Spanish, and Sultan. To be added to this list are practically all the varieties of the following breeds: Brahmas, Campines, Cochins,

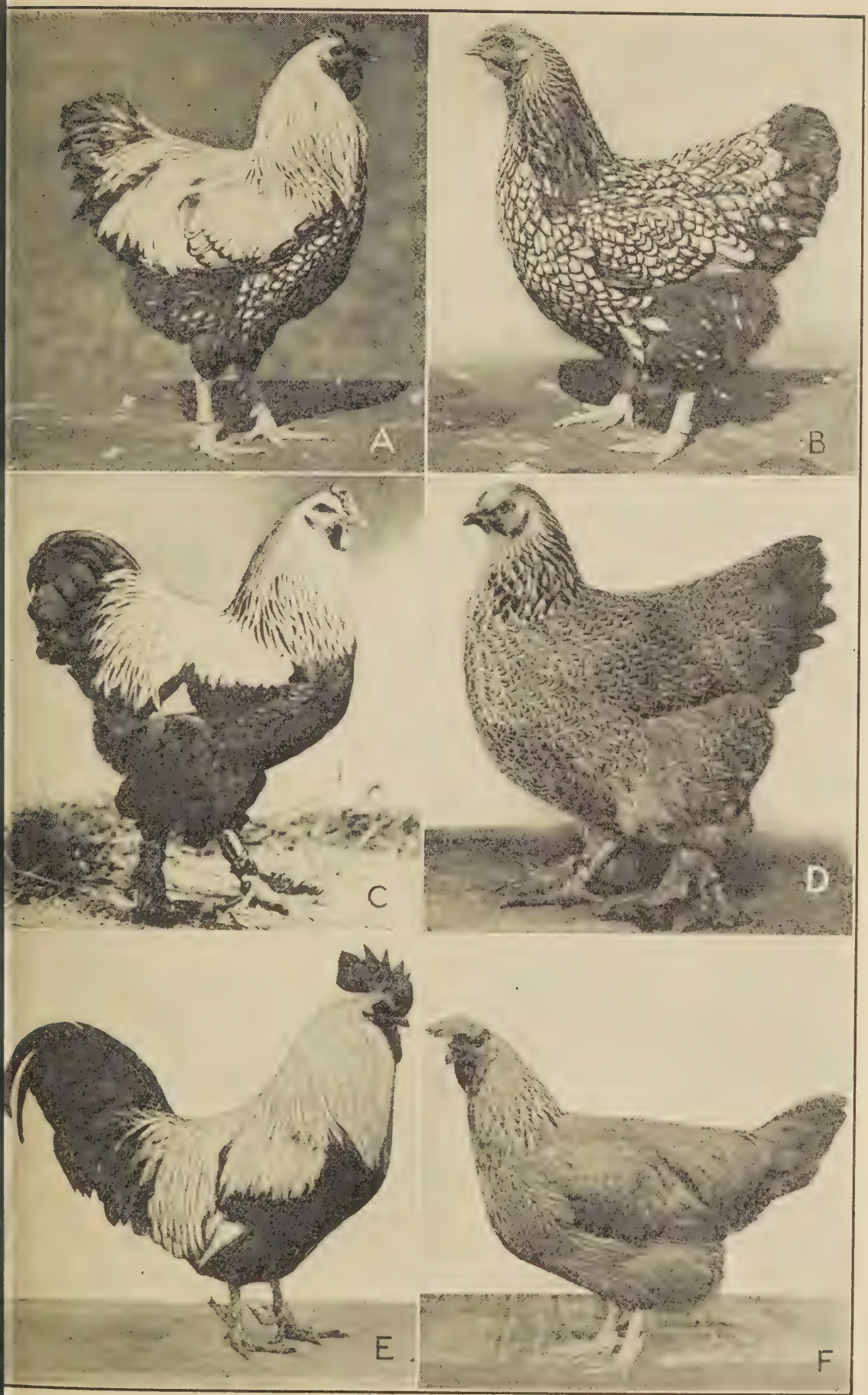

FIG. 4. Sexual dimorphism in plumage pattern in a laced, a penciled, and a ippled variety. Silver-Laced Wyandottes at the top, Dark Brahmas in the iddle, and Silver-Gray Dorkings at the bottom. Except for the lacing on the east and body feathers of the Silver-Laced Wyandotte male and absence of cing in the hackle of the Silver-Gray Dorking male, the three males resemble ch other in appearance. The three females differ considerably, however, among emselves and from the males. (U. S. D. A.)

TABLE 1. THE MORE IMPORTANT CHARACTERISTICS OF VARIOUS BREEDS OF CHICKENS

Breed	Type of Comb	Color of Earlobe	Color of Skin	Color of Shanks	Shanks Feathered or Unfeathered	Color of Egg
Ancona	Single and rose	White	Yellow	Yellow	Unfeathered	White
Aseel	Pea	Red	Yellow	Various	Unfeathered	Brown
Australorp	Single	Red	White	Dark slate	Unfeathered	Brown
Barnevelder	Single	Red	Yellow	Yellow	Unfeathered	Dark brow
Blue Andalusian	Single	White	White	Slaty blue	Unfeathered	White
Brahma	Pea	Red	Yellow	Yellow	Feathered	Brown
Buckeye	Pea	Red	Yellow	Yellow	Unfeathered	Brown
Campine	Single	White	White	Leaden blue	Unfeathered	White
Chantecler	Cushion	Red	Yellow	Yellow	Unfeathered	Brown
Cochin	Single	Red	Yellow	Yellow	Feathered	Brown
Cornish	Pea	Red	Yellow	Yellow	Unfeathered	Brown
Creeper	Single	White	White	Slaty blue	Unfeathered	White
Crevecoeur	V-shape	Red	White	Leaden blue	Unfeathered	White
Dorking (Silver-Gray, Colored)	Single	Red	White	White	Unfeathered	White
Dorking (White)	Rose	Red	White	White	Unfeathered	White
Faverolle	Single	Red	White	Pinkish white	Feathered	Brown
Game	Single	Red	White	Various	Unfeathered	Brown
Hamburg	Rose	White	White	Leaden blue	Unfeathered	White
Houdan	V-shape	White	White	Pinkish white	Unfeathered	White
Java (Black)	Single	Red	Yellow	Black	Unfeathered	Brown
Java (Mottled)	Single	Red	Yellow	Leaden blue and yellow	Unfeathered	Brown
Jersey Black Giant	Single	Red	Yellow	Black	Unfeathered	Brown
Lakenfelder	Single	White	White	Slaty blue	Unfeathered	White
Langshan (Black)	Single	Red	White	Bluish black	Feathered	Brown
Langshan (White)	Single	Red	White	Slaty blue	Feathered	Brown
Leghorn	Single and rose	White	Yellow	Yellow	Unfeathered	White
Malay	Strawberry	Red	Yellow	Yellow	Unfeathered	Brown
Minorca (Black)	Single and rose	White	White	Dark slate	Unfeathered	White
Minorca (Buff and White)	Single and rose	White	White	Pinkish white	Unfeathered	White
New Hampshire	Single	Red	Yellow	Yellow	Unfeathered	Brown
Orpington (Buff and White)	Single	Red	White	White	Unfeathered	Brown
Orpington (Black)	Single	Red	White	Black	Unfeathered	Brown
Plymouth Rock	Single	Red	Yellow	Yellow	Unfeathered	Brown
Polish	V-shape	White	White	Slaty blue	Unfeathered	White
Red Cap	Rose	Red	White	Leaden blue	Unfeathered	White
Rhode Island Red	Single and rose	Red	Yellow	Yellow	Unfeathered	Brown
Rhode Island White	Rose	Red	Yellow	Yellow	Unfeathered	Brown
Silkie	Cushion	Light blue	Blue	Leaden blue	Feathered	Brown
Sussex	Single	Red	White	Horn	Unfeathered	Brown
Welsummer	Single	Red	Yellow	Yellow	Unfeathered	Brown
White-Faced Black Spanish	Single	White	White	Dark slate	Unfeathered	White
Wyandotte	Rose	Red	Yellow	Yellow	Unfeathered	Brown

TABLE 2. STANDARD WEIGHTS OF VARIOUS BREEDS OF DOMESTIC FOWL

Breed	Standard Weight in Pounds			
	Cock	Hen	Cockerel	Pullet
Ancona	6	4½	5	4
Australorp	8½	6½	7½	5½
Brahmas:				
Light	12	9½	10	8
Dark	11	8½	9	7
Buff	11	8½	9	7
Buckeye	9	6½	8	5½
Campine	6	4	5	3½
Chantecler	8½	6½	7½	5½
Cochin	11	8½	9	7
Cornish:				
White-Laced Red	10	8	8½	6½
Dorking:				
White	7½	6	6½	5
Silver-Gray and Colored	9	7	8	6
Faverolles	8	6½	7	5½
Houdan	7½	6½	6½	5½
Java	9½	7½	8	6½
Jersey Black Giant	13	10	11	8
Langshan	9½	7½	8	6½
Leghorns	6	4½	5	4
Malay	9	7	7	5
Minorca:				
Single-Comb Black	9	7½	7½	6½
Single-Comb and Rose-Comb Whites, Rose-Comb Black, and Single-Comb Buff	8	6½	6½	5½
New Hampshire	8½	6½	7½	5½
Orpington	10	8	8½	7
Plymouth Rock	9½	7½	8	6
Redcap	7½	6	6	5
Rhode Island Red	8½	6½	7½	5½
Rhode Island White	8½	6½	7½	5½
Sussex	9	7	7½	6
Spanish, White-Faced Black	8	6½	6½	5½
Wyandotte	8½	6½	7½	5½

Cornish, Dorkings, Hamburgs, Houdans, Javas, Langshans, Leghorns, Minorcas, Orpingtons, Plymouth Rocks, Polish, Sussex, Wyandottes, and several breeds of Bantams.

Other Plumage Patterns. Plumage colors that have not been mentioned are confined for the most part to the Games, Game Ban-

tams, certain other breeds of Bantams, and other breeds such as the Cantonese, Faverolles, Barnevelders, Lakenfelder, and Welsummer. Since practically no investigational work has been undertaken to determine the nature of the inheritance of the color patterns of these breeds and varieties further reference to them is unnecessary at this time.

Similar Color in Both Sexes. In all of the solid-colored breeds and varieties, including the whites, blacks, buffs, blues, and reds, the male and female in each case are of the same color. The same is true in several of the parti-colored breeds and varieties, including those with the following kinds of plumage: barred (except the Silver-Penciled and Golden-Penciled Hamburg), mottled, pied, spangled, and columbian. In some of the breeds and varieties with laced plumage, such as Silver Sebright Bantams, Golden Sebright Bantams, Silver Polish and Golden Polish, Buff-Laced Polish, Blue Andalusians and Blue Leghorns, Orpingtons, and Plymouth Rocks, the sexes have the same color scheme.

Sex Dimorphism in Color Pattern. In numerous breeds and varieties the sexes differ in color scheme, in many cases to a marked extent, giving rise to the expression "sex dimorphism in color pattern." In the Silver-Laced Wyandotte the male is somewhat different from the female, for although practically all of the female's plumage is laced the male has silvery white wing-bows and back. A greater difference exists between the male and female color scheme in those breeds in which the females are penciled, for in this case practically all of the female's plumage is penciled whereas in the male there is no penciling in any part of the plumage. Varieties in which the females are stippled, as in the Brown Leghorn and Silver-Gray Dorking, show an entirely different color scheme in the males.

THE SIGNIFICANCE OF BREED AND VARIETY STANDARDS

The greatest significance arising from the development of breed and variety standards rests in the fact that the buying public demands uniformity in the stock it buys; there must be uniformity of type, color, and productive ability. The next greatest significance in the development of breed and variety standards is the stimulation given to the poultry-breeding industry. Another significant fact is that the numerous characters which different breeds and varieties possess have served as the basis for studies on the inheritance of those characters. The fact that various characters were found to be inherited and that certain combinations of characters could be "fixed" in strains of fowls proved to be a great stimulus to poultry breeders.

In order that poultry breeders might attain the greatest success in their breeding operations it was necessary for them to have an ideal standard in mind at all times. In the early history of the poultry

ndustry, when the production of eggs and poultry meats was not so mportant from the economic standpoint as it is today, it was per- ectly natural that emphasis should be placed upon details of plumage olor and such other characters as type of comb, color of earlobe, and he presence or absence of feathering on the shanks or between the toes.

Poultry breeding as an industry lies at the foundation of poultry usbandry, and the many diversified standard breeds and varieties hich have been produced from a very small number of ancestral orms is striking evidence of the degree to which man has developed nd extended his control over the inheritance of the numerous char- cters which fowls possess. It is a truism that man's fancies have led o the production of many of the standard breeds and varieties at resent existing in many parts of the world, and the satisfaction of aving developed something new has constituted one of the best timuli in man's efforts to understand the laws of inheritance.

In a practical world, however, which we find ours to be, there has een a growing demand for the production of birds that meet man's eeds as well as his fancies. The production of eggs and poultry meat as become of more importance than in former times. Therefore, ore and more is the poultry breeder confronted with the question: ow can one best select and breed his birds for the production of ffspring possessing both standardbred and production qualities?

The importance of breeding birds for beauty as well as utility is early emphasized by Dendy (1929) in the following words: "In ite of the gross materialism of the present age some of us still rejoice the possession of an aesthetic faculty and recognize the existence of ch a thing as beauty." The development of laying strains with a mplete disregard for breed type and other standardbred characters ould mean a great sacrifice in the interests of the art of poultry reeding. Do away with breed and variety standards, and what would appen to the poultry-breeding industry? If breed standards had never een adopted in the beef and dairy cattle, sheep and swine industries, hat would be the present-day condition of these industries?

Whatever the poultry breeder's objective may be, it is a recognized ct that the basis of practically all breeding operations is the breed andard, the ideal shape or type and other characteristics by which e breed is distinguished from another. This is true whether one is reeding poultry for the novel characters they possess or for purely conomic purposes. Although all breeds lay eggs and produce meat, ere are some breeds that have little economic value; for instance, e author used Silkies in some crossing experiments involving the heritance of certain characters and found that the progeny which

inherited the blue or dark purple skin of the Silkies could not be marketed because of the natural prejudice against dressed chickens with such dark skin.

The great majority of poultry breeders of today are interested in the production of eggs or meat, for which purpose they usually breed a standard breed or variety. They are thus interested in maintaining certain breed or variety standards, particularly if they offer for sale hatching eggs, baby chicks, or breeding stock. Although it is necessary to maintain breed standards, it is true that in the early development of many breeds there was a tendency to attach too much importance to certain minor characters and too little importance to characters of economic importance. The most desirable ideal combines the essential characters of the standard for the breed and characters of the greatest economic importance.

Since those who buy hatching eggs, baby chicks, laying pullets, and breeding stock demand a uniform product possessing a certain standard of excellence, and since the poultry breeder who sells hatching eggs, baby chicks, laying pullets, or breeding stock must meet the buyers' demands, it is necessary to consider the minimum requirements that breeding stock must possess in order that the poultry breeder may most readily accomplish his objective.

The great majority of poultry breeders desire to secure the greatest economic returns from their efforts; therefore, not only must their breeding stock conform to the standards of breed type and variety color, but the female breeders must be birds that are good layers of large-sized eggs, and both male and female breeders must give high fertility and hatchability of eggs and produce superior progeny. These are the minimum standards that the poultry breeder must adopt in order to make the greatest possible net income from his poultry-breeding operations.

Suppose that a farmer decides to replace his flock of mongrels with standardbred stock and has expressed a preference for birds with white plumage. As indicated below, he has the choice of several varieties, depending upon the color of skin, the color of egg laid, and whether he wants stock with rose or single combs.

Yellow skin, brown egg, single comb—White Plymouth Rock and others.
Yellow skin, brown egg, rose comb—White Wyandotte.
Yellow skin, white egg, single comb—S.C. White Leghorn and others
Yellow skin, white egg, rose comb—R.C. White Leghorn and others
White skin, brown egg, single comb—White Orpington.
White skin, white egg, single comb—S.C. White Minorca.
White skin, white egg, rose comb—R.C. White Minorca.

If the farmer had a preference for stock with buff or black plumage he would also have the choice of a number of varieties, depending upon the color of skin, color of egg laid, and type of comb.

As far as is known, none of the characters mentioned have any influence on factors of economic importance, such as hatchability and egg production, but the fact remains that most poultrymen want their birds to conform to certain standards. The next few pages are devoted

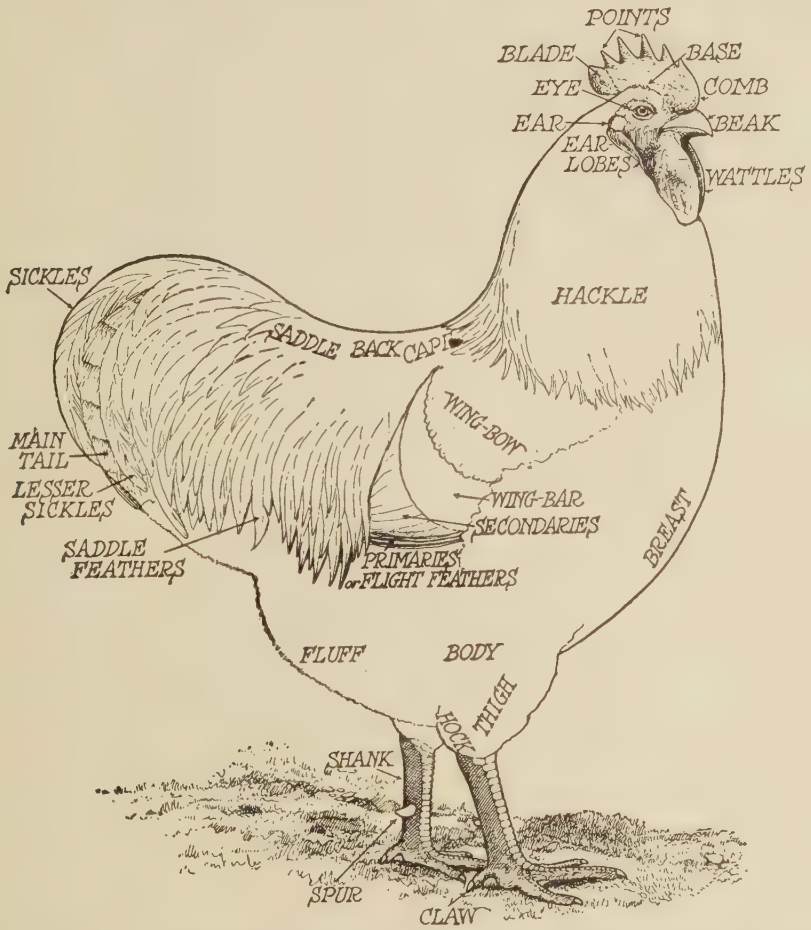

FIG. 5. Glossary chart, giving the names of the different parts of the male fowl. (U. S. D. A.)

to a discussion of some of the more important requirements that birds should meet in order to conform to the standards of the breed and variety the birds represent.

Table 1 gives some of the outstanding characteristics of most of the breeds; Table 2 gives the standard weights for those breeds for which standard weights have been adopted. Among the more important characters by which a standardbred bird should be judged may be included the following: the symmetry of the bird or the degree to which its type conforms to that of the breed it represents, the relative size of the bird, the color of plumage, the kind of comb, and the absence of feathers or tubs on the shanks and toes of breeds having nonfeathered shanks.

These and other characters are discussed briefly in the following pages for the purpose of giving readers some conception of the basic characters a good bird must possess.

Occasionally a bird may possess a character that is objectionable either from the standpoint of appearance or for economic reasons. A crooked keel is objectionable from the economic standpoint in marketing poultry and is considered a serious defect in breeding birds. A crooked back is also objectionable and disqualifies the bird possessing it from being considered a worthy specimen. There are other characters which birds sometimes exhibit, some of them being regarded as defects and others as disqualifications. A number of the more important defects and disqualifications which every poultry breeder should consider in the selection of his breeding stock are discussed in the following pages.

Symmetry. By the term "symmetry" is meant the outline or contour of a bird. Is a certain bird symmetrical in all its parts? Symmetry really refers to feather contour plus the visible parts of the bird such as head and shanks and toes. Symmetry refers to the *tout ensemble* of the bird.

There are two characters that destroy a bird's symmetry and constitute disqualifications, and birds possessing either one should not be used in the breeding pen. One of the disqualifying characters is what is known as "squirrel-tail," a tail projecting forward beyond a perpendicular line drawn through the juncture of the tail and back at a right angle to the line of the back. A squirrel-tail makes a bird very unattractive. The other disqualifying character affecting the symmetry of a bird is what is known as "wry-tail," a tail turning permanently to one side from a vertical position. This character also makes a bird unsightly.

The extent to which the different breeds of chickens differ in body form without the feathers has never been determined, so that at present it is impossible to say that one breed is superior to any other breed for egg production on the basis of body form alone. The relationship between body form and egg and meat production is discussed in Chapter IX.

Size. The matter of size or body weight is an important one from the standpoint of maintaining breed standards. The standard weights of the different breeds have been given in Table 2, and individuals of the different breeds should be expected to attain the approximate weights given for cocks, hens, cockerels, and pullets, respectively.

In the case of Leghorns and Anconas, the standard weight of the cock is 6 pounds and that of the cockerel 5 pounds; if a cock weighs

less than 4.5 pounds or a cockerel less than 3.5 pounds it is considered a disqualified bird. The standard weight of the Leghorn and Ancona hen is 4.5 pounds and that of the pullet is 4 pounds; but if either female falls more than 1 pound under the standard weight it is disqualified.

In all other breeds having standard weights, given previously, any specimen falling more than two pounds below standard weight is disqualified. Care should be exercised against breeding birds that are much below or above the standard weights given for each breed.

The Head and Its Adjuncts. The head is usually the first part of a fowl that catches the eye, so that frequently the appearance of the head creates an impression that is applied to the rest of the bird. A male with a poorly developed or ill-proportioned head creates an unfavorable impression even though the rest of his body may be nigh perfect.

The head and its adjuncts include the beak, skull, eyes, comb, wattles, earlobes, crest, muffs, and beard. The first six characters are common to all breeds and varieties, whereas the last three are found in certain Continental and other breeds.

Beak. The beak should be stout and of good shape, a deformed beak being a disqualification. The Standard of Perfection or the club standard for a breed should be consulted for the description of the ideal shape and color of beak, because, although most breeds have beaks that should be short or medium in length and well curved, there are marked differences between the beaks of such breeds as the Cornish, with its short, very stout, well-curved beak, and the Exhibition Game, with its long, tapering, slightly curved beak. The problem of the color of the beak in relation to egg production in breeds with yellow skin is discussed in Chapter IX.

Eyes. The eyes should be full and bright and of proper color for the breed or variety. Occasionally a bird is found in which one eye is lighter in color than the other eye; such a defect is considered quite serious.

Comb. The types of comb common to each breed or variety have been given in Table 1. The most common type is the single comb, and the next most common is the rose comb. Other types, such as pea, walnut, V-shaped, and strawberry comb, are each common to a few breeds only.

Single combs vary a great deal in size depending upon the breed; for instance, the Cochin has a single comb of small size, the Plymouth Rock and Rhode Island Red each has a single comb of medium size, the Leghorn has a large single comb, and the Minorca has a very large single comb. All single combs should have five points, except the

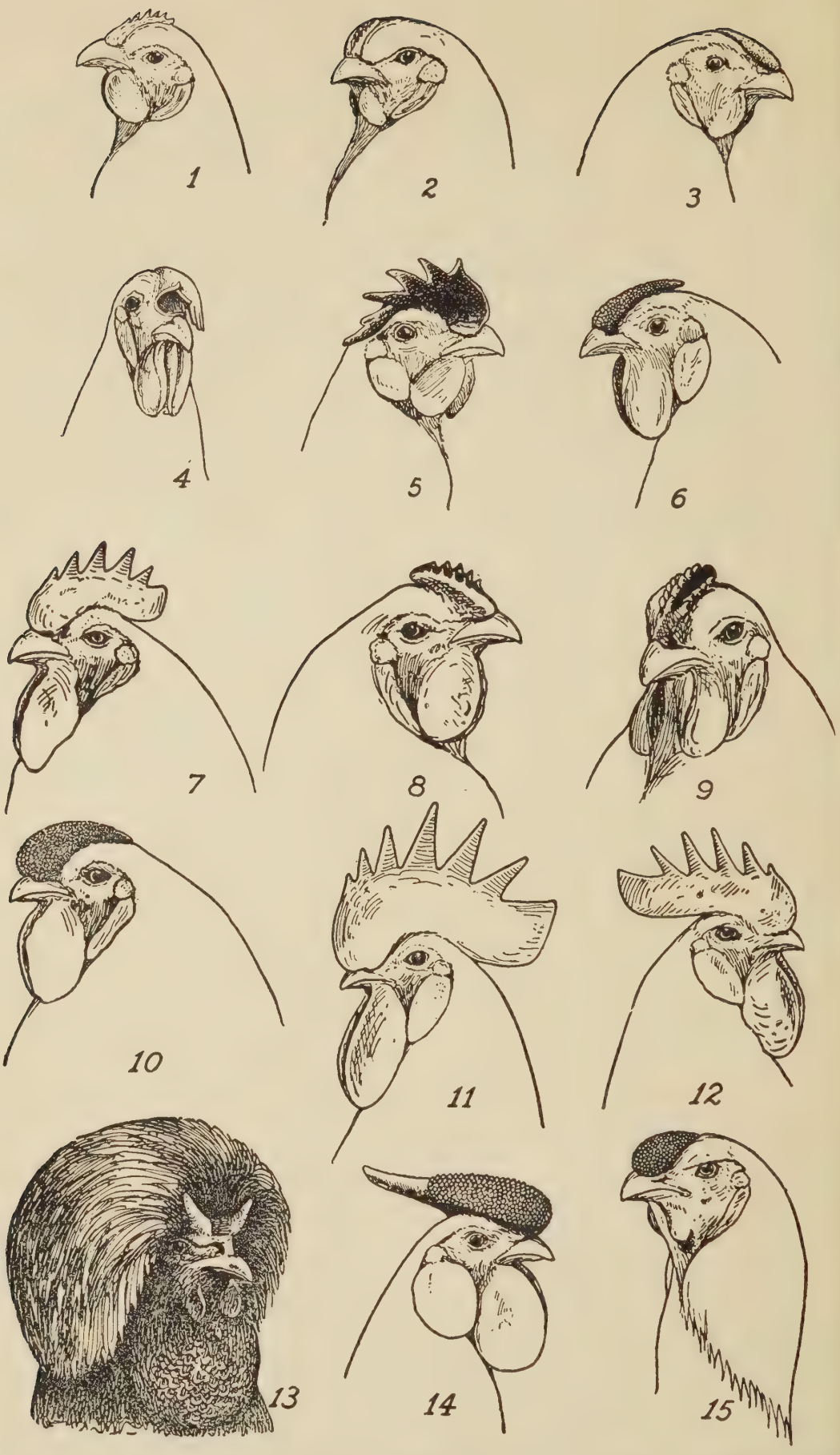

FIG. 6. Ideal types of combs in different breeds. 1 and 7, single (Barred Plymouth Rock and Rhode Island Red); 2, 8, and 9, pea (Brahma); 3 and 10, rose (Wyandotte); 4 and 11, single (Minorca); 5 and 12, single (Leghorn); 6, rose (Rhode Island White); 13, V-shape (Houdan); 14, rose (Hamburg); 15, strawberry (Malay). (U. S. D. A.)

Minorca, which has six. The points in all single combs should be smooth; the third point is the longest and the second and fourth points are longer than the first and fifth. In Mediterranean females the single comb should begin to turn over just back of the second point. The most common defects in single combs include coarseness in texture, too many or too few points, and thumb marks or depressions on the side of the comb. Side-sprigs are a disqualification. A single comb that falls over to one side so that it becomes a lopped comb is a disqualification except in females of the Mediterranean breeds.

Rose combs are found in Wyandottes, Leghorns, Rhode Island Reds, Minorcas, Hamburgs, and other breeds. The size of rose combs varies greatly according to the breed. The points should be smooth and even. In the Leghorns and many other breeds the projection, called spike, at the rear of the comb should extend horizontally, whereas in Hamburgs the spike should incline upward very slightly. The most serious defects in rose combs include coarseness in texture, unevenness in outline, unevenness in the points, a hollow center, and more than one spike on the rear of the comb. A rose comb lopping over to one side of the head sufficient to obstruct the sight constitutes a disqualification. A rose comb so large as to obstruct the sight is also a disqualification.

The other types of comb, such as pea and V-shaped, should be of relatively small size and well proportioned so that the bird's head has a good appearance.

Comb Quality. The quality of the comb in all breeds is a very important matter because a comb of coarse texture is often associated with a bird having a coarse skin. The comb should be firmly attached to the head and in the case of the single comb not too thin, because a thin comb in males is inclined to lop and crack. A comb of soft, velvety texture is an indication of a soft, pliable skin which is desirable in layers.

Wattles. The size of the wattles varies somewhat according to the breed with the exception that the Chantecler is supposed to be without wattles. The wattles of the Plymouth Rock and similar breeds should be of medium size, those of the Leghorn somewhat larger, and those of the Minorca still larger. The wattles should be smooth and of fine texture.

Earlobes. The color of the earlobes is an important matter because, if neglected entirely, breeds with normally white earlobes may have many specimens with a great deal of red in the lobe and breeds with normally red earlobes may have many specimens with much white in the lobe. Positive enamel white in the earlobes of red-lobed breeds, except the Dorkings and Redcaps, constitutes a disqualification. The

change in the pigmentation of the earlobe in relation to egg production in breeds with white earlobes is discussed in Chapter IX.

Shanks and Toes. The shanks and toes of a fowl are of importance from the standpoint of the support they give the body. The shanks should be straight and set well apart, avoiding any appearance of being "knock-kneed" or "bow-legged." The toes should be well formed. The shanks and toes should be of the proper length and color for the breed or variety which the bird represents. Dark spots on the shanks or toes of all breeds and varieties having yellow, white, or pinkish-white shanks or toes, except in the case of Anconas and Houdans, constitute a defect. On the other hand, if the shank or foot of a bird is of a color foreign to the breed or variety it represents, the bird is disqualified.

In all breeds in which nonfeathering of the shanks and toes is normal, the presence of a feather, stub, or feather-like growth on the shank or toe of a bird is a disqualification; in fact, a bird is disqualified if there is unmistakable evidence that such a character has been removed.

Plumage Color and Quality. The color and the quality of the plumage of a bird are of importance in the maintenance of breed and variety standards. Maintaining proper color, so far as possible, is necessary; otherwise the members of a flock may soon lose all semblance of the color pattern of the variety they are supposed to represent. Good quality of feathering is important because it is apparently indicative of good health.

Some breeds differ considerably in the development of feathering: Cochins are noted for loose feathering; Leghorns have closer feathering; the Game breeds have extreme closeness of feathering.

Uniformity in Color Markings Desirable. Some of the more important defects in plumage color and development are mentioned here because the poultry breeder should do everything possible to prevent them from becoming established in his flock. One of the greatest defects in all solid-colored varieties, such as Buff Orpingtons, Black Minorcas, and White Plymouth Rocks, is unevenness of surface color. Among parti-colored varieties, such as Barred Plymouth Rocks, Partridge Cochins, and Silver-Penciled Wyandottes, there is often lack of uniformity in feather markings and in the manner in which the colors of the different sections of the body blend with each other. Among other parti-colored varieties, such as Brown Leghorns, there is frequently a lack of distinctness in feather markings, so that certain sections, such as the hackle in the male and the wing-bows in both

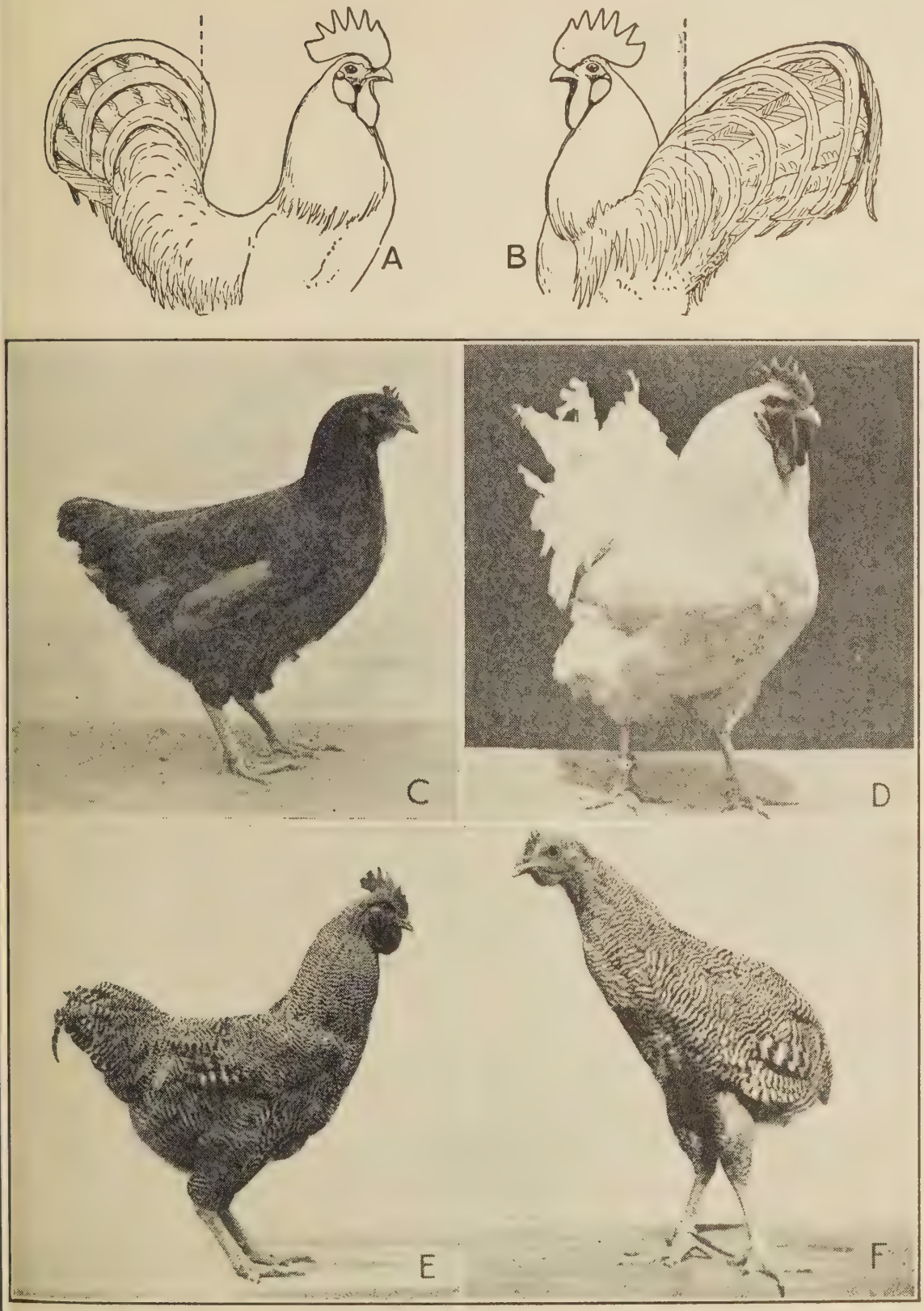

FIG. 7. Common defects and disqualifications. A, squirrel-tail, a disqualification. B, wry-tail, a disqualification. C, split-wing, a disqualification. D, split-tail, a serious defect. E, slipped wing, a disqualification. F, split-wing, poor body type, and weak constitution. (U. S. D. A.)

sexes, may be considerably "off-color" as far as the standard for the variety is concerned.

In white varieties, brassiness, a yellow cast on the surface of the plumage, is objectionable and constitutes a defect. When present, it is most noticeable in the hackle of the male and over the back and shoulders of both sexes. Certain strains of White Leghorns are inclined to show salmon color on the breast of the females. Gray specks and black ticking, sometimes present in white varieties, are defects; brown or black in the quills of the primaries or secondaries of white varieties are disqualifications.

In buff varieties the appearance of black or white in any section of the plumage is a defect, as are also mealiness, light-colored shafting, and slate undercolor.

In black varieties perhaps one of the most common defects is purple barring. The primaries and secondaries of various black varieties sometimes have gray or white tips, both being defects. The presence of red or yellow in any part of the plumage of a black variety is a disqualification.

In red varieties, brassiness, mealiness, and light-colored shafting are defects. In Rhode Island Reds slate undercolor is a defect.

In barred varieties, including Barred Plymouth Rocks, Campines, and Gold and Silver-Penciled Hamburgs, unevenness of barring is a common defect. In Barred Plymouth Rocks, both brassiness and the presence of a black feather are defects.

A defect of a decidedly serious nature is a split tail, giving the tail an unfinished appearance. The defect is usually due to the faulty development of the main tail feathers, causing a gap to appear between them. A twisted feather in the wing or tail of a bird constitutes a disqualification. A wing that has a decided gap permanently developed between the primaries and secondaries is called a split wing, this being a disqualification. A wing in which the primaries are not held in proper position when the wing is folded, thus giving a drooping appearance, is said to be a "slipped wing" and is a disqualification.

For a discussion of the other defects and disqualifications of the various breeds and varieties the reader should consult the American Standard of Perfection, various breed club standards for breeds not recognized by the American Poultry Association, and a valuable discussion on judging by Lamon and Kinghorne (1929).

PROBLEMS

1. Why is it desirable for a poultry breeder to have a definite objective in mind in conducting his breeding work?

2. What is the significance of "breed" in the poultry industry, and how did the numerous existing breeds become established?

3. (*a*) What is the economic significance of the standard weights of various breeds?

(*b*) Mention five of the heaviest breeds.

4. (*a*) What two breeds have red earlobes and lay white-shelled eggs?

(*b*) Is there a breed with white earlobes that lays brown-shelled eggs?

5. (*a*) What is the chief difference in the nature of the penciling in the Partridge Cochin female and the Dark Cornish female?

(*b*) What is the difference in plumage color between partridge and silver-penciled varieties?

(*c*) What is the difference in plumage color between the Silver-Laced Wyandotte male and the Silver-Penciled Wyandotte male?

6. (*a*) What are the defects and disqualifications most commonly encountered in White Leghorns?

(*b*) What are the defects and disqualifications most commonly encountered in Barred Plymouth Rocks?

7. Are the following characters of any economic importance to a poultry breeder who offers breeding stock for sale: comb conforming to the standard, color of earlobe, color of plumage, color of skin, color of egg, and size of bird?

8. Mention five of the most commonly occurring disqualifications.

9. Should a bird with a disqualification be used in the breeding pen?

10. Mention at least 10 varieties having white plumage, 10 having black, 5 having barred, 3 having blue, 3 having silver-penciled, 3 having partridge, and 1 having columbian.

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CHAPTER II

THE PHYSIOLOGY OF REPRODUCTION

The characteristics that distinguish one breed or variety of chickens from another breed or variety are external characteristics easily recognized. The external appearance of a chicken, however, is but the manifestation of certain fundamental processes which take place within the organism.

The inheritance of such characters as combs, spurs, and plumage markings is made possible by virtue of the reproductive system, which is responsible for the production of the male and female reproductive cells. These reproductive cells contain the hereditary elements that give use not only to the external characters which a bird possesses but to other characters as well, including egg production, hatchability, and viability.

The development of the comb, spur, plumage coloration, and other characters is conditioned, to a considerable extent at least, by the products that are elaborated by the organs of the regulatory system. As the result of intensive research during recent years it is apparent that the regulatory system is of far greater significance in avian physiology than has heretofore been realized.

THE REGULATORY SYSTEM

It has long since been known that the numerous activities that take place within the chicken's body are regulated and correlated in order that development may proceed normally and the organism function efficiently. The regulatory system with which the fowl is equipped includes a number of ductless glands, called "endocrine glands," which secrete products called "hormones." These hormones are specific chemical substances that serve as messengers, correlating the activities of one internal organ with those of other internal organs. In other words, a hormone is a gland secretion which when transported to another part of the body, even in very minute amounts, influences a specific physiologic process.

The regulatory system of the chicken includes the following endocrine glands: pineal, pituitary, thymus, thyroid, parathyroids, adrenals, pancreas, ovary, and testes. Each of these glands elaborates

one or more hormones that exercise specific effects in numerous physiological processes, particularly those having to do with the development of secondary sexual characteristics. The structure of these glands has been described in detail by Blatt (1935), but in this discussion it is only possible to give the essential points.

The pineal gland is a small pear-shaped gland, difficult to see with the naked eye, situated at the median line in the transverse fissure at the base of the brain and slightly protruding therefrom. The pituitary gland is situated at the base of the brain and consists of two distinct parts or lobes joined to the base of the brain by a stalk. The anterior lobe of the pituitary, *pars glandularis,* is larger than the posterior lobe, *pars nervosa,* while another part, *pars tuberalis,* is relatively less well developed in birds than in mammals. The principal anatomical features of the pituitary have been described by Fichera (1905), Tilney (1911, 1913), Mitchell (1929), and Rahn (1938, 1939). The thymus gland consists of three pairs of masses of glandular tissue, each about the size of a flattened wheat kernel, situated on the sides of the neck along the course of the carotid artery. The thymus is somewhat larger in males than in females, according to Greenwood (1930), but in both sexes its involution begins about four months after hatching, according to Latimer (1924). The thyroid gland consists of two lobes, situated in the thoracic cavity slightly anterior to the base of the heart. A more detailed discussion of the structure and function of the thyroid gland is given by Chu (1938). The parathyroids are so small that they cannot be seen with the naked eye and are found in conjunction with the thyroid glands. The adrenal glands consist of a pair of triangular glands, each about the size of a pea, situated at the anterior border of the kidney. The pancreas lies between the folds of the duodenum of the intestinal tract. The ovary and the testes will be described in a later section of this chapter.

Leonard and Righter (1936) have shown that as between White Leghorns and English Game bantams, the pituitary of the bantams is relatively heavier, the thyroid is relatively lighter, and the adrenals are approximately the same size. The weights of the endocrine glands of normal-sized birds have been given by Latimer (1924), Juhn and Mitchell (1929), and Landauer and Aberle (1935). In comparing the adrenals, pituitaries, thyroids, and gonads of normal breeds with those of the Frizzle fowl, which differs from other breeds in having a peculiar curling of its feathers, Landauer and Aberle (1935) observed that at hatching time the adrenals, pituitaries, and gonads of Frizzle chicks do not differ from those of normal chicks either in weight or

histological structure. The thyroids of the Frizzle chicks, however, tend to be slightly larger and show greater activity than the thyroids of normal chicks. It is suggested that the increased activity of the relatively larger Frizzle thyroids is related to the accelerated rate of metabolism which is caused by the incomplete insulation of the body.

Hormones Secreted. Research to determine the hormones secreted by the different endocrine glands has made marked progress during recent years although it is still in the embryonic stage. Very little is known concerning the nature of the secretions elaborated by some of the endocrine glands, whereas in the case of other glands it has been determined that several hormones are secreted and much has been learned concerning their effects on different organs and parts.

Van Dyke (1936) has listed a group classification of hormones, some of which are elaborated by the endocrine glands of the chicken while several others are obtained from other animals or are prepared commercially but have been demonstrated to have a pronounced effect in avian physiological processes. Since intensive research is continually discovering hitherto unknown hormones and since the knowledge of the effects of some of the known hormones is being broadened so rapidly, it is only possible to mention here in the space available in this book on poultry breeding some of those hormones which have been demonstrated to have pronounced effects in bringing about sexual differentiation of organs or parts as well as in the functional ability of breeding stock.

Female sex hormones, oestriol or theelol, and oestrone or theelin, have been obtained from the urine of pregnant mares. Testosterone has been obtained from the testes. Androsterone and dehydroandrosterone have been obtained from male urine. There are also commercial preparations, such as androstrin and erugon, obtained from testes and commercial preparations obtained from male urine. Gonan, hebin, and prolan are gonadotropic hormones obtained from pregnancy urine, and autex is a gonadotropic hormone obtained from the serum of the pregnant mare. The pituitary has been shown to elaborate the following five secretions: (1) gonad stimulating hormone; (2) pituitrin, an ovipository stimulus; (3) thyroid stimulating hormone; (4) growth stimulating hormone; (5) prolactin, discussed in considerable detail by Riddle (1938) and Witschi (1937). The thyroid gland secretes thyroxin. The medulla of the adrenal gland secretes adrenalin and the cortex of the adrenal glands secretes cortin. The cortex of the ovary secretes a female hormone and the medulla of the ovary a male hormone.

REPRODUCTIVE SYSTEM

The male and female fowl possess organs for the production and elimination of the reproductive cells, the fertilization of a female reproductive cell by a male reproductive cell being necessary for the development of young. The reproductive cells are produced in the primary sexual organs or gonads and are carried to the exterior by the accessory sexual organs.

The Male Gonads. In the male the gonads consist of a pair of testes, or testicles, from each of which there is a convoluted tube called the "epididymis," which connects with the "vas deferens," which leads to the cloaca. The testes are situated at the anterior ends of the kidneys and are small yellowish-colored bodies frequently pigmented with melanic pigment, according to Bittner (1925). That the left testis is usually larger than the right one has been observed by Thomsen (1911), Firket (1914), Swift (1915), Mimura (1928), and others. Domm and Juhn (1927), however, found that, although this is true in very young birds, the right testis tends to become the larger of the two in older birds. Each testis consists of a large number of slender tubes, called seminferous ducts, from the linings of which the reproductive cells are given off, whence they are conducted to the epididymis, which conducts the reproductive cells to the vas deferens.

The vasa deferentia open into ducts which lie directly over a groove in a rudimentary copulatory organ, according to Hertwig (1926), Dove (1928), Yamaguchi (1928), Taylor (1933), Romanoff (1933), Schroeder (1933), Masui and Hashimoto (1933), Jull (1934), and Gibbs (1935).

It is the presence of this rudimentary copulatory organ in male chicks that makes possible the segregation of chicks according to sex about twelve hours after they are hatched. The sex of most chicks can be determined by the presence or absence of the organ by physical examination, the organ being observed as a small pimple on the lower rim of the vent, midway between the two sides. Most of the male chicks have a relatively prominent organ while in most females it is completely absent. A small percentage of both males and females may have a relatively small prominence or process and considerable training and experience are necessary to be able to distinguish the males from the females. Training schools have been established for training persons in speed and accuracy in sexing chicks at hatching time and those interested should refer to Gibbs (1935) and a set of instructions prepared by the United States Department of Agriculture (1934).

Spermatozoa. During their passage through the epididymis and the vas deferens, the reproductive cells are in suspension in the semen or seminal fluid, which is ejaculated at the time of mating. Burrows and Titus (1939) observed that among crossbred cockerels semen production was just beginning at 222 days of age. It increased gradually until at 275 days of age it averaged slightly more than 1.0 cubic centimeter per bird at each time of collection. The reproductive cells are called "spermatozoa" and according to Craft, McElroy and Penquite (1926), and Hutt (1929) the number of spermatozoa per cubic centimeter of semen varies greatly among males and among ejaculations from the same male. Moreover, Hutt (1929), Penquite, Craft and Thompson (1930), and Sampson and Warren (1940) have shown that the density of sperm suspension bears no relationship to fertility.

The mature spermatozoon of the chicken is long, slender, and cylindrical in form, the posterior end merging into a long tapering tail, according to Payne (1914), and Warren and Kilpatrick (1929). Lack of space prevents a detailed discussion of the different parts of the spermatozoon except to say that, according to Adamstone and Card (1934), the head contains globules of fatty material which serve as a supply of food material with which to support the activities of the spermatozoon until it is in a position to fertilize the yolk of the egg. The long tail provides the spermatozoon with the power of motility which enables it to traverse the oviduct of the female.

The fertilizing capacity of a spermatozoon is only possible after it has gone through certain ripening or maturation processes while it progresses from the testis through the epididymis and vas deferens. Munro (1935, 1938*b*, 1938*c*) has shown that in a sexually active male the sperm requires only about twenty-four hours to pass from the testis to the rudimentary copulatory organ and that practically all of the maturation processes are passed through while the spermatozoon is traversing the vas deferens. Hogue and Schnetzler (1937) demonstrated that at about sixteen weeks of age Barred Plymouth Rock cockerels produced spermatozoa that were capable of fertilizing the yolks of eggs.

The Female Gonad. The reproductive system of the female consists of an ovary and oviduct. The ovary is involved in the production of the female reproductive cells called "ova" and the oviduct transports the ova from the ovary to the cloaca and secretes albumen, membranes, and shell, which nourish and protect the embryo. The ovary, or female gonad, is located on the left side of the body, although during embryonic development a right gonad and oviduct also develop but gradually degenerate until at hatching time only rudiments remain.

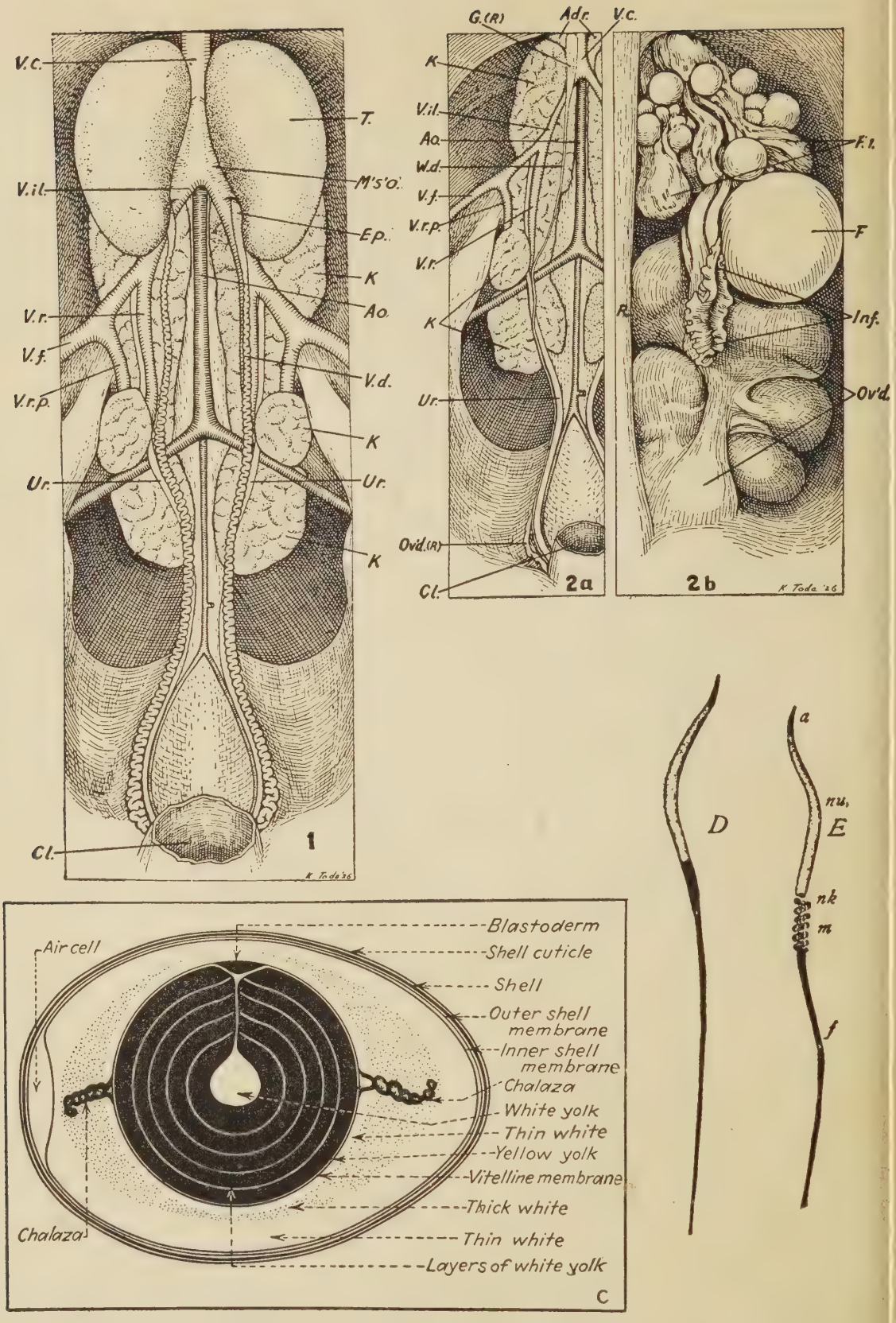

FIG. 8. The reproductive organs and cells of the domestic fowl. 1. The reproductive organs of the male: T, testis; V. d., vas deferens; Cl., cloaca. 2a. Right side of female: G(R), rudimentary gonad; Ov'd(R), rudimentary oviduct. 2b. Left side of female: F.l, ovulated follicles; F, mature follicle; Inf. Infundibulum or mouth of the oviduct; Ov'd., oviduct. (After Domm.) C. The egg or reproductive cell of the female. The blastoderm is popularly called the germ-spot. (Modified from Schaible, Davidson, and Moore, 1936.) D and E. The reproductive cells of the male, popularly called sperm; in this illustration they are much enlarged, relatively.

The observations of Brode (1928) led him to conclude that a rudimentary right ovary is always present in the female chicken.

A few cases have been reported, however, showing both a right and left ovary and oviduct present in the adult fowl. A right ovary in addition to the normal left one has been observed by Brandt (1889), Gadow (1891), Chapellier (1913), and Hertwig (1930). A functional right ovary and right oviduct in addition to the normal left ones have been observed by Kirkpatrick and Card (1916), Crew (1931), Wodzicki (1934), and Alder (1939).

The left gonad is situated to the left of the median line of the body just posterior to the lungs and at the anterior end of the kidney, and is attached to the dorsal wall of the body cavity. In an inactive con-

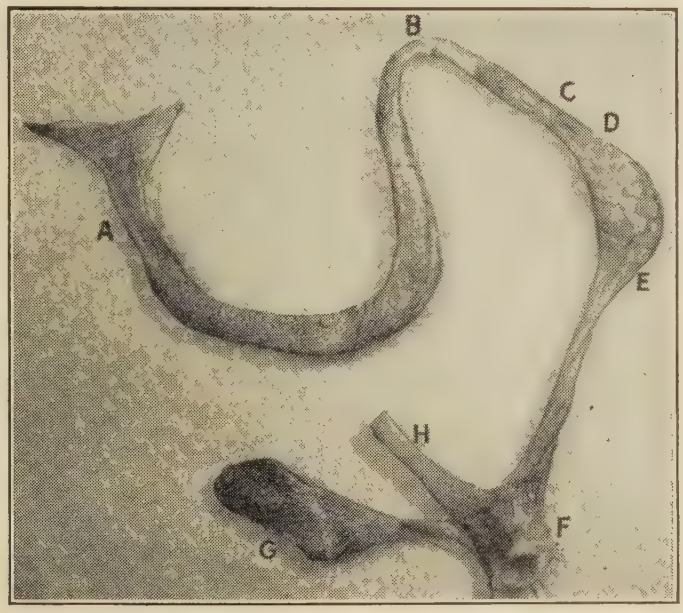

FIG. 9. The more important regions of the oviduct are as follows: mouth; A to B, the magnum; B to C, the isthmus; C to E, the uterus; E to F, the vagina; G, the rudimentary right oviduct; H, the large intestine. (Asmundson and Burmester, 1936.)

dition, as in the case of an immature pullet, the gonad appears as a whitish mass of irregular material, whereas in an active condition it appears as a yellowish cluster of cells of varying size.

The Oviduct. The oviduct is a coiled tube extending from the region of the ovary to the cloaca and occupies a considerable portion of the abdominal cavity of the hen. According to Curtis (1910), the anterior end of the oviduct is spread out beneath the ovary so that it is a simple matter for the oviduct to grasp the ova after ovulation has taken place.

Surface (1912), Asmundson (1931), and Warren and Scott (1935*a*) have described the oviduct as being comprised of the following six

parts: (1) mouth; (2) funnel; (3) magnum; (4) isthmus; (5) uterus; (6) vagina. According to Surface (1912) the oviduct is comprised of seven layers of tissue.

From the observations of Surface (1912), Giesberg (1923), Shibata (1931), Tisima (1933), Richardson (1935), and Warren and Scott (1935), it is apparent that the following figures represent the approximate length in centimeters of each of the sections of the oviduct of a hen in laying condition: mouth, 5; funnel, 4; magnum, 33; isthmus, 10; uterus, 12.0; vagina, 12. Buckner and Martin (1929) have shown that the oviduct of a hen not in laying condition is only about one-half as long as the oviduct of a hen in laying condition.

THE FORMATION OF THE EGG

The ovum consists of finely granular protoplasm enclosed in a pellicle called the "vitelline membrane." Each ovum begins as a microscopic point in the ovary and is contained in a very thin envelope called the "follicle," which is attached to the ovary by a slender stalk or pedicel.

Pearl (1912) observed from 914 to 3,605 ova in various stages of development in different hens, but the number present in any individual appears to bear no relationship to her laying ability, although Pearl and Schoppe (1921) observed a general relationship between the average number of ova present and egg production in different orders of birds.

The observations of Pearl and Schoppe (1921), Domm (1927), and Steggerda (1930) to the effect that removal of part of the ovary is followed by complete regeneration of the ovary and, in some cases, increased egg production were not confirmed in critical tests by Card and Roberts (1931) nor by Hutt and Diedrich (1933).

In the course of their development the ova apparently pass through three different stages or periods. The first period, which is one of multiplication, takes place while the embryo is developing in the incubated egg and ends about hatching time, according to Lillie (1919). Following the multiplication period there is a period of slow growth, which begins about the fourteenth day of incubation, according to d'Hollander (1904), and extends throughout the life of the bird. During this period of slow growth each ovum gradually increases in size until it reaches a diameter of about 6 millimeters. Riddle (1916) divides this period of slow growth into two phases. During the first phase the ovum attains a diameter of 3 millimeters, and during the second phase the increase in diameter is up to 6 millimeters. After the ova have attained a size of 6 millimeters in diameter a few at a time

undergo a very rapid increase in growth, their diameter being increased on the average about 4 millimeters every day for about eight days until the full size of approximately 40 millimeters is attained.

Warren and Conrad (1939) found that the rate of growth of the ovum was relatively constant from the ninth to the seventh day prior to ovulation but decreased rapidly after the seventh day. The daily increments in the amount of yolk secreted increased rapidly from the ninth to the fourth day prior to ovulation but decreased rapidly after the third day preceding ovulation. Yolk-size variations among eggs of different hens and among eggs of the same hen were not associated with different growth rates of ova, from which it was concluded that variations in yolk size are due to differences in the period of growth rather than in rate of growth.

The increase in the size of the ovum is due to the assimilation of yolk material which is comprised of innumerable spheres of white yolk and yellow yolk. According to Lillie (1919), the spheres of white yolk are smaller than those of the yellow yolk, the former ranging from tiny granules up to about 0.07 millimeter and the latter ranging from about 0.025 to about 0.100 millimeter in diameter.

The yolk material is conveyed to the ovum by the highly vascular follicle and enters by diffusion. Romanoff (1931) has shown that the growth of the ovum is marked by a very rapid increase in the percentage of dry matter, which reaches the highest point in the mature ovum. The fat and calcium content of the ovum also increase during the growth of the ovum, whereas the density, hydrogen-ion concentration, iodine value, and refractive index of the extracted fat show only slight changes.

From the very beginning of its development the ovum contains a nucleus. Originally the nucleus is in the center of the ovum but as the ovum grows through the accumulation of yolk material, the nucleus migrates to the uppermost periphery of the ovum and lies beneath the vitelline membrane. In an infertile egg the nucleus is known as the germ spot and in a fertile egg as the germinal disc, which later develops into the blastoderm.

The yolk material is deposited in the ovum in concentric layers, beginning with a layer of white yolk immediately surrounding the germinal disc or blastoderm and beneath it to form a thin-necked, flask-shaped structure, the spherical portion of which is in the center of the ovum. This flask-shaped structure is called the "latebra." According to Riddle (1911) the white yolk material is deposited in thinner layers than the yellow yolk material, the white yolk being deposited during the night, a period of low blood pressure, and the yellow yolk

being deposited during the day, a period of high blood pressure in the laying hen. Conrad and Warren (1939) have shown, however, that alternate layers of white and yellow yolk are never found in eggs laid by hens fed *ad libitum* an all-mash diet. They state that the yolk of the latebra is different from yellow yolk in chemical properties and presumably in the mechanism of its formation. Birds fed large amounts of feed rich in xanthophyll, especially during short periods, lay eggs containing alternate white and yellow layers of yolk. Conrad and Warren observe that the fat in the laying hen's diet containing the xanthophyll-rich feeds is deposited in the ovum until used up, after which the bird synthesizes fat from the dietary carbohydrate and protein, this synthesized fat probably containing no yellow color since the bird is unable to synthesize carotenoid pigments. Conrad and Warren also observed that the accumulation of yolk material apparently proceeds at the same rate day and night.

The Formation of the Vitelline Membrane. The vitelline membrane is of composite structure, as shown by Lécaillon (1910*a*, 1910*b*, 1910*c*). It comprises a delicate noncellular layer immediately surrounding the ovum, outside of which is a layer of degenerating epithelium, and outside of that again a layer of albumen secreted by the oviduct.

Ovulation. When the ovum attains its mature size, approximately 40 millimeters in diameter, it is ready to be liberated from the ovary. Its liberation or ovulation is made possible by the rupture of the follicle along a streak called the "stigma." Subsequently the ruptured follicle degenerates. According to Curtis (1914*a*) the internal pressure due to continued yolk formation is probably the most important factor which causes the follicle to rupture. Since ovulation usually takes place within about half an hour after the time of laying an egg, the act of laying an egg may serve as a stimulation to the liberation of an ovum from the ovary, although some other stimulus must be involved in the case of the laying of a pullet's first egg as well as in the case of two ova liberated from the ovary at approximately the same time, as occasionally happens. Warren and Scott (1935*a*) have suggested that the time of ovulation probably is regulated by the sequence of maturation of the ova rather than by the expulsion of the previous egg. Ovulation usually takes place between 5 A.M. and 2 P.M.

Phillips and Warren (1937) observed that the mean period of time elapsing between oviposition and ovulation was 32.2 minutes. A positive correlation was found between the length of interval between eggs and the time intervening between oviposition and ovulation, thus indicating that the length of interval between eggs and the period between

the laying of an egg and the ovulation of the next egg are directly associated. Apparently pressure resulting from the prolonged tension of the muscle fibers of the follicular membrane is one factor responsible for ovulation, but the cause of the stimulation of these muscle fibers was not determined.

Warren and Scott (1934) have observed that the mouth of the oviduct may grasp the ovum prior to ovulation, but more usually ovulation takes place and then the mouth of the oviduct engulfs the ovum, even if it has dropped into the body cavity. Warren and Scott (1935*a*) have stated that the grasping of the ovum by the mouth of the oviduct is entirely at random. Having entered the oviduct, the ovum passes down that organ by the ciliary action according to Cushny (1902), Harper (1904), and Mimura (1937) and by the peristaltic movements of the walls of the oviduct, as described by Gadow (1891), Patterson (1910), Pearl and Curtis (1912, 1914), and Warren and Scott (1935*a*).

The Secretion of Albumen. During its passage down the oviduct, the ovum is surrounded by albumen, secreted by the glands of the oviduct, which have been described by Surface (1912), Bradley (1928), and Richardson (1935). The differentiation of the albumen into four distinct layers occurs, for the most part, after the ovum has entered the uterus, although some differentiation usually starts in the isthmus. About 40 to 50 per cent of the total albumen is secreted in the magnum section of the oviduct, about 10 per cent in the isthmus, and about 40 to 50 per cent in the uterus. Approximately 90 per cent of the total protein in the albumen of the completed egg is secreted by glands in the magnum section of the oviduct.

The four distinct layers of albumen are: (1) two chalazae consisting of twisted strands of thick albumen attached at opposite poles of the ovum, the chalaza at the large end of the egg having a clockwise twist and the chalaza at the small end of the egg a counterclockwise twist, the chalazae being attached to a thin layer of albumen of similar density surrounding the yolk; (2) an inner layer of thin albumen which comprises about 20 to 25 per cent of the total albumen; (3) a layer of thick albumen which comprises about 50 to 60 per cent of the total albumen; (4) an outer layer of thin albumen which comprises about 20 to 25 per cent of the total albumen.

Practically all the thick albumen is secreted in the magnum section of the oviduct, apparently under the stimulus of the presence of the ovum. According to Chomkovic (1927), Hansen (1934), and McNally (1934) practically all of the solid matter in the albumen is secreted in the magnum. The solids of the albumen consist of proteins except for

a fraction of about 1 per cent of ash and certain other substances. Asmundson and Burmester (1936) have shown that the posterior half of the magnum is largely responsible for the secretion of the thick albumen. Moreover, they suggested that their observations may have some bearing on the height of the goblet secreting cells of the glands of the magnum, as reported by Bradley (1928).

Cole (1938) has shown that the goblet cells in the glands of the magnum, particularly in the posterior half of the magnum, secrete mucin fibers, which are a characteristic constituent of thick albumen. In the anterior portion of the magnum the cells averaged 11.4 μ in height whereas in the posterior part they averaged 30 μ in height. According to the observations of Lorenz, Taylor and Almquist (1934), Knox and Godfrey (1934, 1938), and Van Wagenen and Hall (1936), the per cent of thick albumen in eggs has a genetic basis, a problem discussed in detail in Chapter VIII.

According to the observations of Conrad and Scott (1939), it is apparent that soluble proteins are secreted by the magnum at a steady rate during intervals between the passage of successive eggs through the oviduct. They have suggested that this accounts for the fact that the first egg of a clutch contains more white than successive eggs of the same clutch.

Hansen (1934) and Asmundson and Burmester (1936) have shown that thick albumen secreted in the magnum is of a gelatinous nature without evidence of chalazae. As the ovum with its gelatinous envelope of thick albumen progresses through the isthmus of the oviduct, some of the thick albumen becomes partially liquefied, apparently due to the effects of the mechanical movements of the oviduct on the ovum and the albumen. According to Conrad and Phillips (1938), the liquefaction of a portion of the thick albumen is due to colloidal change that takes place.

According to McNally (1933), the chief difference between thick and thin albumen is due to the presence of a protein called mucin in thick albumen and the almost complete absence of mucin in thin albumen. Similar observations were made by Schaible, Moore, and Davidson (1935). Hektoen and Cole (1925) observed that mucin is apparently the only protein present in thick albumen responsible for its gel-like structure. Romanoff (1929), Almquist and Lorenz (1933), and Almquist (1936) have submitted evidence indicating that the difference between thick and thin albumen is not of a chemical nature.

According to Warren and Scott (1935) and Conrad and Phillips (1938), there is a marked increase in the formation of the inner layer

TABLE 3. APPROXIMATE LENGTH OF DIFFERENT SECTIONS OF THE OVIDUCT, APPROXIMATE PERCENTAGE OF ALBUMEN SECRETED IN EACH OF THREE SECTIONS, AND APPROXIMATE TIME SPENT BY THE YOLK IN DIFFERENT SECTIONS

(Compiled from data of Warren and Scott, 1935, and Asmundson and Burmester, 1936)

Section of Oviduct	Approximate Length, Centimeters	Percentage of Albumen Secreted	Approximate Time Spent by Yolk
Mouth	5.0		
Funnel	4.0		18 min.
Magnum	33.0	40 to 50	2 hr. 54 min.
Isthmus	10.0	10	1 hr. 14 min.
Uterus	12.0	40 to 50	20 hr. 40 min.
Vagina	12.0		

of thin albumen about five hours after ovulation has taken place. The ovum has reached the uterus section of the oviduct, the formation of the inner layer of thin albumen and the appearance of the chalazae at this time being due to the rotation of the ovum about its long axis, according to Almquist (1936) and Conrad and Phillips (1938). The white yolk material surrounding the germinal disc is of higher specific gravity than the yellow yolk, which constitutes the major portion of the ovum, so that the germinal disc inclines to remain at the top of the ovum. The ovum is of higher specific gravity than the albumen, so that as the ovum is rotated about its long axis within the layer of thick albumen the mucin fibers are wrapped around the egg to form the chalaziferous layer and the chalazae; at the same time the inner layer of thin albumen with its decreased mucin content is formed. Observations made by Burmester and Card (1939) indicate, however, that the formation of chalaza in yolkless eggs cannot be accounted for on the same basis as in the case of normal eggs. According to Burmester, Scott, and Card (1939*a*), the rate of increase in uptake of uterine secretion is maximal immediately after the egg has reached the uterine pouch and decreases uniformly to a minimum level in eight hours.

Scott and Burmester (1939) found that by resecting separately the anterior, middle, and posterior portions of the albumen-secreting region of the oviduct the absolute amount of white secreted was reduced, the difference being significant when the middle and posterior portions were resected. The absolute amount of thin white secreted was reduced

significantly by resecting the anterior and posterior portions. The absolute amount of thick white was reduced significantly by resecting the middle and posterior portions. Eggs laid by hens from which the anterior portion was removed contained significantly more thick white than eggs laid by the same hens prior to the operation.

The Secretion of the Shell Membranes. Surrounding the albumen of the egg are two white membranes known as the inner and outer shell membranes, which lie in close juxtaposition except at the large end where they are separated to form the air cell. Both membranes are composed of matted organic fibers of protein crossing one another in all directions.

As early as 1847 Coste showed that the shell membranes are secreted by glands in the isthmus section of the oviduct, an observation confirmed by Pearl and Curtis (1912) and by Asmundson (1931*a*) as a result of his findings upon resecting a part of the isthmus. Hays and Sumbardo (1927) observed that the inner membrane is much thinner than the outer one. As pointed out by Asmundson and Burmester (1936), they are secreted in the isthmus section of the oviduct.

From the observations of Hughes and Scott (1936), and Scott, Hughes and Warren (1937) it is concluded that there is no augmentation of nitrogen to the egg through the shell membranes, this observation being confirmed by Asmundson and Burmester (1938). McNally (1934) secured evidence, however, that indicated that ovoglobulin is added to the egg while it is in the uterus.

Beadle, Conrad, and Scott (1938) point out that the secretion produced by the glands of the uterus is a mineral solution consisting of sodium, calcium, and potassium, present as chlorides and bicarbonates. The potassium concentration of the uterine secretion is about ten times that of normal blood serum. The permeability of the shell membranes permits the mineral solution to be incorporated in the egg to form the outer layer of thin albumen.

The shell membranes usually show a pinkish tinge, which Klose and Almquist (1937) have shown to be due to the presence of a pigment called "oöphorin."

The Secretion of the Shell. Material for the formation of the shell of the egg is secreted in the uterus section of the oviduct, as indicated by the observations of Pearl and Surface (1909), Pearl and Curtis (1914), and Richardson (1935). The shell is composed of four layers and a cuticle, or bloom. The innermost layer consists of minute calcareous particles; the second layer consists of minute particles of calcium carbonate; the third, or mammilla, layer consists of large

spheres of calcite; the outer layer is composed of crystals of calcium carbonate arranged with their long axes perpendicular to the surface as pointed out by Needham (1931). The cuticle, or bloom, on the outside of the egg, is apparently structureless. The four layers of the shell and the bloom are porous, thus allowing for the passage of air and moisture. The conception of shell porosity apparently originated with Landois (1865) and was elaborated upon by Surface (1912) and Lillie (1919).

From the observations of Rizzo (1899) and Hays and Sumbardo (1927), it is apparent that egg shells vary considerably with respect to their porosity, the latter investigators recording from 413 to 601 pores per square centimeter in the equatorial region of the egg. Romanoff (1929) observed that a thick shell has a large number of small pores whereas a thin shell has fewer pores, though some are quite large.

That the pores of the egg shell are sealed with an organic material was proposed by Nathusius (1868) and subsequently confirmed, with modifications by Rizzo (1890), Clevisch (1913), and Almquist and Holst (1931). A condition of normal shells in which an uneven translucency is due to localized concentrations of moisture, largely independent of the pores, has been described by Holst, Almquist, and Lorenz (1932). An abnormal type of shells, termed "glassy" because when tapped they emit a musical clink like that which results when glass vessels are tapped, has been described by Almquist and Burmester (1934), the thickness and shell porosity being lower than in normal shells. Egg-shell porosity appears to be quite uniform for the eggs of each hen, as pointed out by Almquist and Holst (1931).

The dry matter of the shell consists of approximately 94 per cent calcium carbonate, 1 per cent magnesium carbonate, 1 per cent calcium phosphate, and 4 per cent of organic material, chiefly protein.

Burmester, Scott, and Card (1939*b*) found that the rate of deposition of calcium carbonate is relatively slow during the first three hours after the egg enters the uterus but then increases and very soon attains a constant rate which is maintained until the twentieth hour, when the egg is laid.

Shell Pigmentation. Several breeds of chickens lay eggs that are free of any trace of pigment, while most other breeds lay eggs with brown shells and at least one South American breed lays eggs with blue shells. Although Sorby (1875) mentions seven substances that are probably responsible for egg-shell color, it seems quite certain that one type of pigment, the principal representative of which is oöphorin, is responsible for the brown color in brown-shelled eggs. In a paper by

Punnett (1933) it is suggested that the "banded occyan" listed by Sorby is responsible for the blue color of the South American breed

Shell Thickness. The shells of eggs laid by different hens frequently vary somewhat in thickness as shown by a number of workers From the observations of Romanoff (1929) and Stewart (1936), it appears that the average thickness may vary from 0.30 to 0.40 millimeter. According to the observations of Taylor and Martin (1928) and Taylor and Lerner (1939), thickness of egg shell is an inherited characteristic.

Shell Breaking Strength. That there is a relationship between shell thickness and breaking strength has been shown by Herroste (1916), Romanoff (1929), Morgan (1932), Swenson and James (1932), Almquist and Burmester (1934), Stewart (1936), and Lund, Heiman, and Wilhelm (1938). The average breaking strength was found to be 4.46, 4.81, and 4.75 kilograms respectively, by Romanoff, Stewart, and Lund *et al.*

Egg Shape. From the standpoint of shape, most eggs are ovate with one end larger and more blunt than the other. Although the eggs laid by a flock of hens may differ markedly in shape, the eggs laid by an individual possess a characteristic shape. A review of the theories held by various investigators concerning factors affecting the shape of eggs is given by Asmundson (1931). In 1933 Asmundson and Jeris concluded that egg shape is determined, for the most part, by the time it has left the isthmus section of the oviduct. Klodnits Kii (1935), among others, has supplied evidence showing that egg shape is an hereditary characteristic.

Abnormal eggs and their development are discussed in Chapter VIII.

Egg Size. The size of an egg obviously is determined by the collective weights of its component parts. From various observations on eggs laid by different flocks it may be said that on the average the albumen contributes approximately 59 per cent, the yolk approximately 30 per cent, and the shell approximately 11 per cent of the total egg weight. Many investigations have been conducted on factors affecting the size or weight of eggs, many of the details of which are discussed in Chapter VIII. Here it need only be mentioned that two factors of major importance in determining the size of eggs laid by birds of all ages are the size of the yolk that is formed and the size of the oviduct of the bird.

The Egg at Time of Laying. So far the formation of the egg has been followed from the time the ovum entered the oviduct until the fully formed egg is ready to leave the uterus. The vagina takes no part in egg formation, as pointed out by Asmundson (1931).

Greenwood (1935) concluded from numerous observations that up to the time that a pullet lays her first egg her oviduct has a vascularized membrane which tends to prevent the passage of the egg from the vagina to the cloaca. Asmundson, Gunn, and Klose (1937) have shown, however, that perforation of the vagina may be reduced from the normal age of about 140 days in the pullet to about 42 days by prolonged injections of mare gonadotropic hormones or oestrin, thereby indicating that passage of the egg is not necessary to accomplish perforation.

The completed egg is essentially a reproductive cell. In the higher organisms all life is perpetuated through the egg. The development of the embryos of mammals takes place within the body of the female, whereas the development of the chick embryo takes place, for the most part, outside the female body. It is for this reason that the chicken egg is such a large reproductive cell as compared with the egg of a mammal.

The structure of the egg is such that it provides protection against injury to the embryo, which develops from the blastoderm of the fertile egg. The yolk is the major source of nourishment for the embryo during its early period of development, after which the albumen is the principal source of nourishment.

The following is the approximate composition of the egg, the figures given being percentages of the wet weight:

	Water	Protein	Fat	Ash
Whole Egg.....	65.5	11.8	11.0	11.7
Yolk.....	47.5	17.5	32.5	2.0
Albumen.....	87.0	11.0	0.2	0.8

The act of laying an egg usually requires a few minutes only, the completed egg passing from the uterus through the vagina and being expelled by the eversion of the cloaca. It is interesting to note that the act of laying takes place, for the most part, between 7 A.M. and 4 P.M., the great majority of eggs being laid in the morning. When, however, laying occurs late in the afternoon, the ovulation of the ovum in the succeeding egg is delayed, as observed by Scott and Warren (1935*b*). Other details concerning the time factor in laying and related problems are discussed in Chapter VII.

From the time of Aristotle there has been much speculation concerning which end of the egg is laid first. Although Aristotle (324 B.C.) and several others have observed that the egg was laid with the large end first, their observations appear to have been few in number. Among those who have made numerous observations, Fleischhauer (1926),

Eber (1929), and Krzywanek (1929) came to the conclusion that the egg is laid either with the large or small end first. Olsen and Byerly (1932), reported that among eggs laid by Single-Comb White Leghorns approximately 90 per cent were found in the uterus with the small end caudad, or pointing posteriorly, and among eggs laid by Single-Comb Rhode Island Reds approximately 85 per cent of the eggs were found in the uterus with the small end caudad. About 70 per cent of the Leghorn eggs and about 80 per cent of the Red eggs were laid small end first. It has been suggested by Olsen and Byerly that some of the eggs may become turned end for end as they emerge from the uterus as a result of the small end of the egg protruding into the blind posterior sac of the uterus beneath the vaginal orifice.

Hormones and Egg Production. Nearly all birds lay at a higher rate in the spring of the year than at other times, rate of laying referring to the number of eggs per month or for any given period. It is interesting to observe that for birds in the same latitude in different parts of the world the seasonal curves of egg production are quite similar, as shown by Whetham (1933). The reason given for the increase in the rate of laying during the spring months is that the birds respond to the gradual increase from day to day in the amount of daylight or sunlight. It has been demonstrated that the anterior lobe of the pituitary secretes a hormone that provides a stimulus for the development of ova. The activity of the pituitary gland is influenced by the action of light, the bird's eye being sensitive to the intensity of illumination. Under condition of increasing light, more of the hormone is secreted, and this substance circulating in the blood stimulates the ovary to increased production.

Much evidence has been accumulated during recent years to show that cyclic growth changes of the oviduct are controlled by secretion elaborated by the ovary. Goodale (1916) and Domm (1924, 1927, 1929) have shown that the complete removal of the ovary results in the oviduct becoming much reduced in size, with few or no convolutions. It has been further shown by Domm and Gustavson (1929) and Juhn and Gustavson (1930) that the oviduct of the ovariotomized fowl and of the juvenile female and the resting oviduct of the adult respond to the administration of oestrin, a female sex hormone. The dependence on the ovary of the oviduct for its conditioning has been demonstrated by Rowan (1931) and Bissonnette (1930, 1936), who showed that light acts as a regulating factor in the activity of the ovary. This dependence of the oviduct on the ovary has also been demonstrated by Domm and Van Dyke (1932) and Domm (1935, 1937) by injections of extracts of anterior pituitary into immatur

female fowls. It was found in all cases that the stimulated ovary led to the enlargement and activation of the oviduct.

Experiments on certain wild birds conducted by Bissonnette (1930, 1932, 1933, 1936) indicate that increased length of lighting periods, increased light intensities, and increased amounts of long-waved red light increase sexual activity. Rowan (1936) observed that ultra-violet light is ineffective in stimulating egg laying.

That light exercises a rather pronounced effect on the complicated mechanism of egg laying has been demonstrated by an interesting series of experiments carried on by Warren and Scott (1936). It was first observed that under conditions of normal lighting birds rarely laid any eggs between 5 P.M. and 6 A.M., thus suggesting the operation of some regulatory mechanism which prevents the laying of eggs at night. It was found, however, that when birds that had been under normal lighting conditions were given continuous artificial lighting by using 100-watt Mazda lamps, with no daylight, the laying period was reversed; *i.e.*, whereas under normal lighting the birds laid in the daytime, after seven days of continuous artificial lighting they tended to shift their laying more to the night period. Then when the day period was darkened and artificial light was provided at night, the shift in laying during the night period was almost complete, especially four days after the change. When twenty-four hours of darkness intervened, followed by another shift back to normal daytime lighting and night darkness, the shift to laying in the daytime was almost complete, especially three days after the shift had been made. In other words, under normal daytime light and night darkness hens lay in the daytime; under continuous artificial light, they lay throughout the day; under reversed periods of daylight and darkness, they lay at night; and under continuous artificial light supplemented by daytime normal light, they lay in the daytime.

Since the intervals between layings are usually more than twenty-four hours, successive eggs are laid somewhat later each day. When this results in a bird due to lay after the middle of the afternoon, oviposition usually does not occur and a day's rest results, according to Warren and Scott (1936). A new series is started with morning laying. The interruption in laying was found to result from a delay in ovulation, rather than as the result of retardation or interruption of the progress of the egg through the oviduct. Changes in the lighting conditions were not reflected immediately in the fowl's laying but were expressed after about sixty hours. Thus, the regulating effect of light on laying probably has its influence on the later stages of the maturation of the ovum.

Pearl and Surface (1914*b*) found that ovulation ceased when large doses of *corpus luteum* were injected intraperitoneally, but that smaller doses showed little effect. Fresh anterior pituitary substance injected intraperitoneally by Walker (1925) inhibited ovulation. The resting ovaries of molting hens were not activated by extracts of the anterior lobe of the pituitary in experiments conducted by Pearl and Surface

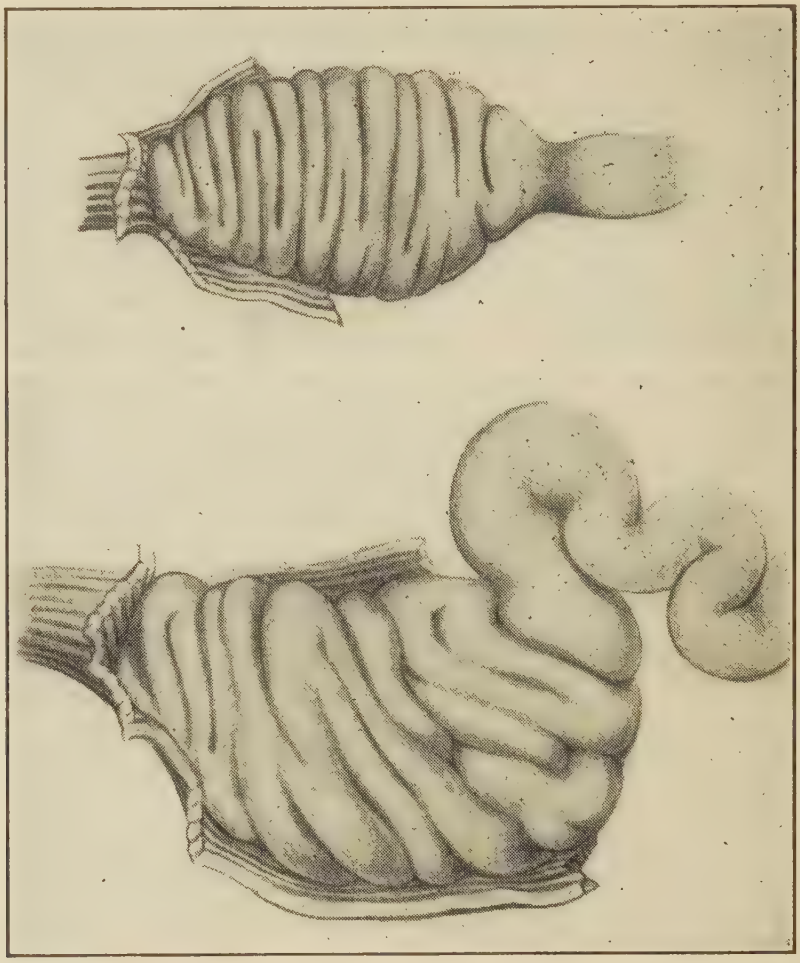

Fig. 10. Upper view, showing the effect on the oviduct of administering oestrone to the incubating egg from which the pullet was hatched; the eggs laid were without shells. Lower view, normal oviduct. (Greenwood and Blyth, 1936.)

(1915) and Pearl (1916). On the other hand, Gutowska (1936) observed that the administration of pituitary anterior lobe to laying hens induced marked changes in the reproductive organs. The prolonged per-oral administration of large doses of the anterior lobe of the pituitary stimulated the activation of the ovary and oviduct.

The injection of pregnant mare's serum into immature pullets by Asmundson and Wolfe (1935) resulted in an increase in the weight of the ovary and oviduct. By injecting hormones into newly hatched chicks, Breneman (1936) observed that the ovaries were stimulated, pregnant mare's serum and follicle-stimulating hormone inducing a

greater response than luteinizing hormone and pregnancy urine. Asmundson, Gunn, and Klose (1937) have shown that by injecting separately pregnant mare's serum and oestrin into immature pullets, pregnant mare's serum caused an enlargement of the ovary and oviduct, and oestrin an enlargement of the oviduct.

Theelin, a female sex hormone, has been shown to affect the growth of the oviduct by Juhn, D'Amour, and Gustavson (1930) and Raspopova (1935). Greenwood and Blyth (1936) demonstrated the pronounced effects of oestrone on the development of the oviduct.

The feeding of small amounts of desiccated thyroid to pullets led Asmundson (1931*b*) to conclude that the size of eggs was apparently reduced or that the eggs did not increase in weight as would be expected normally. It was observed that the size of the yolk was affected more than the albumen and shell. Further work was carried on by Asmundson and Pinsky (1935), desiccated thyroid being fed in such amounts as to supply approximately 1 milligram of thyroid iodine per 1,750 grams of body weight to Leghorn pullets that had commenced laying. Yolk weight was reduced, shell weight was increased, but there was no effect on the amount of albumen secreted. The reduced size of yolk resulted from a retarded growth rate in the ovum. Complete removal of the thyroids resulted in decreased egg production, according to Winchester (1939). The injection of thyroxin into these thyrodectomized birds resulted in increased egg production, whereas thyrodectomized birds not injected with thyroxin continued to lay poorly.

Soli (1911) claimed that the removal of the thymus gland resulted in the production of eggs without shells. Similar results were reported by Riddle (1924*a*). On the other hand, Ackert and Morris (1929) and Greenwood and Blyth (1931) have shown quite conclusively that such is not the case.

From the observations of Altmann and Hutt (1938), it is concluded that the ovary secretes a hormone which stimulates the parathyroid glands; these, in turn, secrete a hormone which leads to a marked increase of calcium in the blood in anticipation of the increased calcium requirements of the hen for the formation of egg shells.

Riddle, Bates, and Lahr (1935) have shown that the injection of prolan, a hormone secreted by the anterior lobe of the pituitary, into the fowl will induce broodiness. Burrows and Byerly (1936) observed that the pituitaries of broody hens contained more prolactin than the pituitaries of laying hens and males. Byerly and Burrows (1936) observed that the pituitaries of laying hens and males of broody genetic

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constitution contained more prolactin than the pituitaries of hens and males, respectively, of nonbroody genetic constitution.

THE PHYSIOLOGY OF SEXUAL DIFFERENTIATION

The development of the fertilized egg into a fully formed chick and later into an adult possessing male or female characteristics is a problem of fundamental importance to a proper understanding of the role of avian physiology in reproduction. The fertilized egg results from the fertilization of the ovum shortly after it enters the oviduct. The act of copulation between male and female brings about the union of a spermatozoon and an ovum. At the time of copulation the male ejects semen containing spermatozoa into the vagina of the female, the spermatozoa traverse the oviduct, and one spermatozoon fertilizes the germ spot or reproductive cell within the ovum.

Approximately three hours after it is fertilized the germ spot divides into two cells. Cell division continues and gives rise to the formation of the germinal disc. The cleavage process of the germinal disc gives rise to the formation of the blastoderm, a structure having two layers, the outer layer comprising the ectoderm and the inner layer the entoderm.

When the egg is placed under suitable conditions of incubation, the blastoderm develops rapidly and extends over the surface of the yolk. The two-layered structure soon gives rise to a three-layered structure, the mesoderm arising between the ectoderm and entoderm. The ectoderm gives rise to the skin, feathers, and other external features as well as the nervous system. The mesoderm gives rise to the blood, bones, muscles, and the reproductive and excretory organs. The entoderm gives rise to the respiratory and secretory organs and the linings of the digestive tract. Such is a gross picture of the development of the embryo during the period of incubation, which normally occupies twenty-one days.

The fertility of incubated eggs can be detected with a high degree of accuracy after about fifteen hours of incubation, according to Olsen and Knox (1938). An ordinary commercial candling "lamp" equipped with a 75-watt daylight bulb was employed, and the candlers found that a pair of dark blue glasses was helpful. Fertility could be detected even after three and four hours of incubation, but candling large numbers at about fifteen hours was determined to be more practical. It may be well to note at this time that the development of the embryo ceases when the egg is in a temperature below 68° F.

It has been pointed out by Lillie (1919) that, with the aid of a microscope, the sex of an embryo can be determined at about the

one hundred and fifty-sixth hour of incubation. The male and female gonads, described in the previous section of this chapter, arise in a structure known as the gonad rudiment, which consists of two distinct constituents of rather diverse origin, the cortex and the medulla. The cortex gives rise to the female gonad; the medulla gives rise to the male gonad. It has been observed previously that the reproductive organs arise from the mesoderm, germ cells occurring in the epithelium formed from the mesoderm.

The beginnings of sexual differentiation is indicated by the thinning or thickening of the germinal epithelium, the thinning into a single layer indicating differentiation in the male direction whereas a thickening to form several layers of cells indicates a differentiation in the female direction. Also, as observed by Willier (1932), the formation of only one set of sex cords from the germinal epithelium is an indication of differentiation into a male gonad, whereas the formation of two sets of sex cords is an indication of differentiation into female gonads. Swift (1916) has pointed out that the single set of sex cords in the male gonad or testis remains attached to the germinal epithelium for a longer period than in the female. Although Firket (1914) suggested that in the female the primary sex cords disappeared, it is known now from the work of Brode (1928) that they persist in modified form. In experiments on the regeneration of the testis of the fowl, Hooker and Cunningham (1938) concluded that somatic cells can transform into germ cells.

In both sexes the left gonad grows more rapidly than the right but after sexual differentiation begins, the left gonad of the female continues to grow much more rapidly than the right gonad whereas in the male there is a tendency for the development of the two gonads to progress at more nearly the same rate.

Secondary Sexual Characters. In the development of every embryo rudiments of sex characters are developed other than the gonads and their accessory ducts, such as the vasa deferentia in the male and the oviduct in the female. These other sex characters develop into what are known as "secondary sexual characters" and include the voice of the bird, its comb, feather structure and plumage coloration, skeletal development, and the presence or absence of spurs. It is well known that the sexes differ with respect to these and many other characters, the differences between the sexes in plumage coloration and body weight having been observed in Chapter I.

Aside from the fact that the male crows and the female cackles, the voice of the male differs from that of the female, sex dimorphism in the syrinx having been discussed by Myers (1917) and Appel

(1929). The comb of the male is usually more prominently developed than in the female. The lower neck, saddle, sickle, and tail feathers are longer in the male, and the first three kinds of feathers are more pointed in the male than in the female. There is a number of breeds, especially in the partridge-colored, silver-laced, and silver-penciled varieties, in which there is sexual dimorphism in plumage color, the male and female plumage descriptions having been given in Chapter I. There is also sexual dimorphism in skeletal development, as pointed out by Schneider and Dunn (1924), Hutt (1929*a*), Maw (1935), and Lerner (1937). Consequently there are sex differences in body weight of adult birds, which also takes into consideration sex differences in rate of growth. Most adult males have spurs, whereas it is unusual for a female to have spurs.

It is customary for males to dominate females, but among the female members of a small flock there is usually a definite social organization wherein certain females dominate others. One hen in a small flock may "boss" all the other females of the flock. Recent investigations have led to the suggestion that the social status of the females of a flock is established by what is called the "peck-order." The observations of Schjelderup-Ebbe (1922, 1935), Masure and Allee (1934), Murchison (1935), Allee and Collias (1938), Sanctuary (1939), and Allee, Collias, and Lutherman (1939) reveal the fact that females ranking high in social hierarchy tend to peck those of more lowly rank very frequently. That social dominance is apparently related to hormone secretions is indicated by the experiments of Allee, Collias, and Lutherman (1939), who were able to modify the social standing of the females in small flocks of adult hens and in flocks of young pullets by administering male sex hormone.

The fact that the mature male and female fowls differ in the number of red blood corpuscles, or erythrocytes, that they contain has been demonstrated by Blacher (1926), Chauduri (1926), and Juhn and Domm (1930). Chauduri observed an average of 4,500,000 red blood corpuscles per cubic millimeter in mature males and an average of 3,127,000 in mature females. Manoiloff (1922–23) devised a chemical test for sex which may be made on the blood. This test is based upon oxidative reactions, a color difference being found to exist between males and females. Steele and Zeimet (1925) devised a simpler test than Manoiloff's and found that it could be applied not only to the blood but also to the pulp of the growing feathers.

Hormones and Comb Development. According to Hardesty (1931), the comb first appears between the sixth and seventh days of embryo development as an elevation of the ectoderm to form the

definitive epidermis, which, as in the skin, becomes differentiated into three layers. The dermis, which underlies the epidermis, becomes modified about one month after hatching to form three layers: (1) a peripheral layer of compact connective tissue; (2) an intermediate layer of loose connective tissue between the fibers of which is mucoid material; (3) a central layer or core of connective tissue bundles and blood vessels. About six weeks after hatching, male and female combs in Leghorns are differentiated, the dermis of the male comb being much more highly differentiated than that of the female comb. From about six weeks to maturity the rate of growth of the male comb is greater than the growth of the body of the bird, this condition being spoken of as heterogonic growth. The female comb, on the other hand, exhibits isogonic growth up to about four months of age, since comb growth progresses at the same rate as that of the body of the bird. After four months in Leghorns, female comb growth becomes heterogonic, growing faster than the male comb of the same age. The turgidity of the male comb, as compared with the female comb, is due largely to greater abundance of mucoid material.

When a male bird is castrated before three months of age, the testes being removed by an operation, the comb fails to develop, due to the fact that no mucoid material is formed, as shown by Hardesty (1931). If castration is performed after sexual maturity has been attained the comb regresses until it finally attains the small size characteristic of the typical capon. Measurements of the rate of regression have been reported by Goodale (1916*e*), Pézard (1918), Zavadowsky (1922), and Finlay (1925).

The regression of the male comb following castration is prevented by transplanting into the body cavity testis tissue obtained either from the bird operated upon or from other birds, as indicated by the results secured by Pézard (1920), Caridroit (1926), and Appel (1929). Testicular extracts injected into capons also prevent the regression of the comb if the injection is made shortly after castration and restores the comb to the turgid condition of a normal cock comb if the injection is made after regression has been allowed to take place. The literature on these experiments is reviewed by McGee, Juhn, and Domm (1928).

The restoration of the capon comb to the cock condition by the injection of testis hormone was also demonstrated by Hardesty (1931), who observed that the hormone produces its effect by stimulating the secretion of mucoid in the comb. The standardization of preparations of male hormone by the comb growth method was investigated by Greenwood, Blyth, and Callow (1933), androsterone being used. Greenwood and Blyth (1935) found that injections of androsterone

directly into the substance of the capon's comb produced a greater response than when the same dose was injected intramuscularly in the pectoral region. Hain (1938*a*, 1938*b*), in experiments on the regression of the comb of Old English Game bantams following castration, concluded that abnormally high temperatures in the spring lowered the average comb-growth response under the influence of androsterone. Wolff and Wolff (1937) found testosterone to be six times more active on the capon comb than androsterone. Emmens (1938) demonstrated that the comb growth of Brown Leghorn capons was restored in size equal to normal cocks in about forty days by intramuscular implantations of tablets of compressed testosterone propionate.

Burrows, Byerly, and Evans (1936) demonstrated that the combs of day-old chicks are quite sensitive to androsterone and another male hormone, testosterone. Marked development of the baby chick comb following the injection of a male hormone was also demonstrated by Dantchakoff and Kinderis (1937). The application of androsterone in oil to the comb region was employed by Frank, Klempner, and Hollander (1938) in a test for the male sex hormone, and Danby (1938), using day-old White Leghorn chicks, observed that the chick comb test could be considered reliable for the assay of male hormones, the sex of the chick having no influence on comb response. Breneman (1938*b*) observed that dihydroandrosterone was more effective than testosterone propionate in promoting comb growth.

The problem of the physiology of the growth and development of the comb has been approached from the standpoint of comb transplantations. From the observations of Kozelka (1929), and Hardesty (1931), it is concluded that comb tissue may be grafted on almost any part of the body, Hardesty securing best results with combs grafted subcutaneously to the region beneath the wing. Grafting a comb on to some part of the same bird is much more liable to be successful than grafting a comb on to some other bird. If a bird with a grafted comb is castrated, the comb regresses but grows again if male hormone is injected.

Judging from the results secured by Souba (1923), Finlay (1925), Greenwood and Crew (1927*b*), and Blyth (1928), it is apparent that in the male the growth of the comb coincides with the increased activity of certain cells in the testes. Breneman (1938*a*) has shown that comb growth in White Leghorns from hatching time to the thirtieth day of age is not primarily correlated with testis weight but that the testis begins secreting a male hormone at a very early age. Moreover, the results secured by Domm (1931*a*) and by Domm and Van Dyke (1932*a*) indicate that the anterior lobe of the pituitary

ecretes a hormone that stimulates the development of the testes. The xperiments of Hill and Parkes (1935) indicate that the anterior lobe of ne pituitary secretes a hormone which influences the functioning of the nyroid gland, and Greenwood and Chu (1939) have presented evidence urporting to show that the thyroid gland secretes a hormone that imulates the gonad-stimulating function of the anterior lobe of the ituitary.

It is well known, from the observations of Domm (1930) and thers, that young cockerels raised indoors without access to sunlight sually have much larger combs than their full-brothers that have ad access to sunlight. Womack, Koch, Domm, and Juhn (1931) have tated that light retards comb growth. Buckner, Insko, and Martin 1932) have shown that White Leghorn cockerels raised in confine- nent without access to sunlight in battery brooders developed abnor- nally large combs and smaller testes than cockerels raised in colony rooders and having access to sunlight. It was also shown that among ockerels raised in confinement without access to sunlight those which ad had their combs removed at four weeks of age developed larger attles and testes than those from which the combs had not been moved. On the other hand, among cockerels having access to nlight those which were allowed to retain their combs had larger stes than those from which the combs and the combs and wattles ad been removed. It was also shown that the removal of the combs f pullets at four weeks of age apparently had no effect on the size of ne ovaries up to the fourteenth week.

In the female the growth of the comb is coincident with the ncreased activity of the ovary, the cortex of which secretes a female ex hormone whereas the medulla of the ovary secretes a male ormone, according to Domm (1931*b*), Domm and Van Dyke (1932*b*), nd Greenwood and Chu (1939). As the hen approaches laying ondition the comb enlarges and becomes more turgid as a result of ne increased activity of the ovary but "lops" to one side, due to the symmetrical lateral increase in the number of connective-tissue fibers, s shown by Champy and Kritch (1926). The increased turgidity, nough not reaching the level observed in the cock's comb, is due to ne secretion of mucoid in the intermediate layer of the comb as the sult of the influence of the male hormone, according to Hardesty 1931). When egg production ceases, the female comb regresses ecause less and less mucoid is secreted. The comb of the nonlaying en may be compared with the comb of the capon, the injection of the male hormone having practically no effect.

Spur Development. In the capon the spurs usually grow longer and are more slender than in the normal male. Goodale (1916), Pézard (1922), Benoit (1923), Zavadowsky (1922, 1926), and Domm (1927) observed that spurs always develop in the female following ovariotomy, the removal of the ovary. From this it appears that spurs develop best in the complete absence of the gonads and that the ovary inhibits spur development more completely than the testis. Bond (1937) has described old Brown Leghorn hens each having a spur on the right or left leg, which may perhaps be accounted for in the decreased functional activity of the ovary.

Kozelka (1929, 1932*b*) has shown that the spurs from either sex grafted to the male host were of the male type, for the most part, whereas on the female host the spur retained the characteristic spur type of the donor. Kozelka (1933*a*) secured evidence indicating that once the chick is hatched the male sex hormone does not influence the female spur. Apparently sexual dimorphism in spur development is due primarily to a genetic difference, as observed by Goodale (1925).

Feather Structure and Plumage Pattern. In all breeds of the domestic fowl, except a few "hen-feathered" breeds, the plumage of the sexes differs considerably with respect to the structure of the feathers over certain parts of the body. In the male the neck, back, and tail feathers are longer and more pointed than in the female, as shown in Chapter I. In the hen-feathered breeds, such as the Campine, the feathers over all parts of the body of the male are the counterpart in shape to those of the female.

In many of the parti-colored breeds and varieties there is sexual dimorphism of plumage pattern because of the fact that the hackle and saddle feathers of the male differ in color from the neck and back feathers of the female. In some breeds and varieties the breast and body feathers of the male also differ from those in the female. Some varieties exhibiting sexual dimorphism in plumage pattern to an outstanding degree include the Brown Leghorn, the Dark Brahma, the Partridge Cochin, Plymouth Rock, and Wyandotte, the Silver-Penciled Plymouth Rock and Wyandotte, and the Silver-Gray Dorking.

During recent years a tremendous amount of research work has been carried on to determine the underlying causes of sexual differences in feather structure and color pattern, the Brown Leghorn having been used to a greater extent than any other variety. Lack of space in a book of this kind prevents a detailed discussion of all the research results secured, but sufficient of the results are discussed to give those interested in poultry breeding some conception of the influence of the gonads and hormones on feather structure and plumage pattern.

The Origin of Feathers. The feather germ, from which the eather develops, arises in the embryo about the fifth day of incubation y a massing of the mesodermal cells under the epidermis. These cells re very shortly broken up into little hillocks, as described by Davies 1889), which are the papillae of the future feather germs. The verlying epidermis next undergoes a thickening and becomes several ayered. Each papilla, together with the epidermis covering it, becomes longated into a cylindrical papilla, which gradually sinks into a epression formed at its base and becomes enclosed by a follicle.

Each feather is formed from a thickened ring or "collar" of epiermal cells at the base of the feather papilla. The shaft or rachis of he feather is formed from the dorsal side of the collar. The vane of the eather is composed of two lateral halves fused to the rachis. Accordng to Juhn and Fraps (1936), the halves of the developing vane ttached to the collar are continually flowing from the mid-ventral ne in opposite directions and uniting dorsally to the rachis.

The barbs, which are outgrowths from the collar, are formed arallel to one another and grow by additions to their bases. Juhn nd Fraps (1934*a*) observed that the rate of barb growth decreased ontinuously from a maximum value at the point of origin to a inimum value at the dorsal limit of the collar and that the curve of arb growth rate is highly important in the determination of pattern.

Lillie and Juhn (1932, 1938) have estimated that about ten days re required for the completion of the growth of the barbs from the iddle of the vane of the breast feathers of Brown Leghorns.

The order of formation of the shaft and barbs is apico-basal; in ach barb the apex at the margin of the feather is the first to be formed nd the distal end, attached to the shaft, is the last to be formed. There re thus two time gradients in each feather, (1) from apex to base along he shaft and (2) from margin to center along the barbs.

According to Juhn, Faulkner, and Gustavson (1931), the growth ate of the rachis is approximately uniform during the formation of the ane, and, according to Lillie and Juhn (1932) and Fraps and Juhn 1936), the growth rate of the barbs decreases from apex to base.

The principles involved in feather growth gradients are of the tmost importance in relation to the type of feather and the plumage attern that develops under certain conditions. The feathers of ifferent body areas have different growth rates, as Juhn, Faulkner, nd Gustavson (1931) have pointed out. They show, for instance, hat in the male Brown Leghorn the growth rate of feathers increases rogressively in the following four areas: back, saddle, anterior breast, nd posterior breast. This means that feathers in different parts of the

bird's body may respond differently to various stimuli, such as hormones liberated by the endocrine glands. The saddle feathers grow more slowly than the breast feathers and, therefore, have a lower threshold of reaction to certain hormones. Differences in growth rates of feathers in different areas with the consequent variations in thresholds of reactions to hormones account to some extent for the sexual dimorphism of feather structure and plumage pattern in several breeds and varieties.

Feather Tracts. Although feathers cover practically all parts of the adult bird's body, they arise from certain defined areas of the skin called "feather tracts" or "pterylae." In the normal chicken there are ten of these feather tracts, as shown in Fig. 37. The areas between the feather tracts are called "apteria."

According to Holmes (1935), the order of the feathers in the feather tracts of the adult bird is determined in the embryo, each feather tract as it arises in the embryo having a specific order. The order of the feather tracts from the standpoint of the appearance of feathers and the order of feathering within each feather tract have been discussed in considerable detail by Chu (1938–1939). It is important to keep in mind that in a male bird the feathers of one tract frequently show a striking difference in shape and coloration as compared with the feathers of another tract. So also, the feathers of the same tract in both sexes frequently exhibit marked structural and coloration differences.

Succession of Plumages. In the domestic fowl there are the following four successive plumages from hatching time to the adult bird: down, chick, juvenile, and adult. For a detailed discussion of the order of the appearance of these four types of plumage, the reader should consult Goodale (1916), Domm (1927), and Chu (1938–1939).

The down is the primary feather type developed by the chick and first appears on the embryo about the tenth day of incubation. At hatching time the chick is completely covered with down, but it is subsequently replaced by definitive feathers, complete replacement of the down being a very gradual process. This covering of definitive feathers is known as the chick feathering stage.

According to Chu (1938–1939), before the down has been completely replaced by chick feathering, the latter is gradually replaced by juvenile plumage, the onset of which is first visible at about six weeks of age. The change from juvenile to adult plumage is a gradual process, due to the orderly manner in which feathers are molted and replaced. There is thus a continuous series of growing feathers within each tract. The molting of the adult plumage which usually takes

lace toward the close of the first laying year follows an orderly equence, as pointed out in Chapter IX.

Gonads and Plumage Development. The castration of the male, y removing the testes, is spoken of as "orchotomy," an operation hich has been demonstrated to result in certain significant changes in ne plumage. Although Sellheim (1898), Foges (1903), Pézard (1911, 918), and Goodale (1913, 1916) concluded that orchotomy produced o significant changes in plumage, the results secured by Zavadowsky 1922), Finlay (1925), Benoit (1929), and Horowitz (1931, 1934) now clearly that the feathers over the entire body of the capon are nger than in the normal male, especially the primary coverts, hackle, addle, and sickle feathers. Champy and Demay (1935) observed that ne castration of crested males resulted in the shedding or incomplete evelopment of the feathers of the crest. The general conclusion ncerning the effects of orchotomy on plumage development is that ne testes exercise a certain degree of inhibition on the expression of ormal male plumage.

When a male of one of the hen-feathered breeds, such as the ebright bantam, is castrated the female-type plumage is replaced y normal male-type plumage, as shown by Morgan (1915–1920), ézard, Sand, and Caridroit (1924), Roxas (1926), Eliot (1928), nd others.

It has been demonstrated that testicular tissue added to ovarian ssue in females does not produce any change in the female plumage. oring and Pearl (1918), Cole and Lippincott (1919), Parkes and rambell (1926), Cole (1927), and others have shown that, when the vary of a female is affected by a tumor or in some other abnormal ay, the female develops cock feathering. Gates (1918) and others ave reported cases of females developing head furnishings and spurs naracteristic of males, such changes being nearly always due to some bnormal condition of the ovary. Gatenby and Brambell (1924) escribed a White Leghorn completely henny except for its cock-like ead, which courted but attacked other hens and crowed frequently; n its left side there was an ovary full of scar tissue and it contained sticular tubules.

A case of double change in sex appearance has been reported by IcCance and Walton (1930). A Light Sussex pullet which had laid up the time she was about one year old, thereafter gradually assumed ale plumage, grew spurs, and mated with other hens. In the spring f her third year, she was seen going to the nests, became broody, and cubated eggs placed under her. In the late spring of her fourth year,

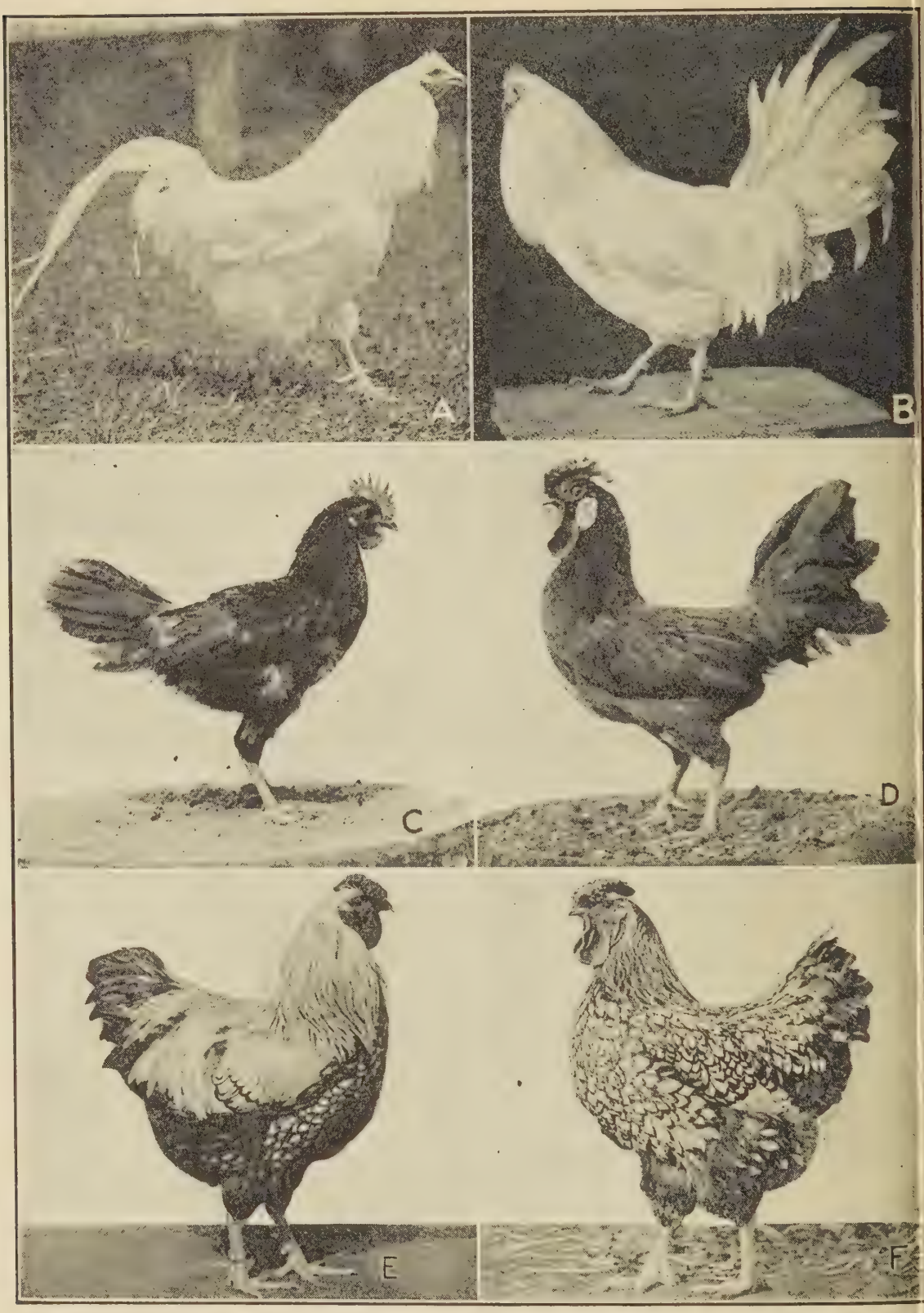

FIG. 11. Males acquire different plumage under different circumstances. A, a capon, resulting from the removal of the testes. (U. S. D. A.) B, a developmental capon, no operation having been performed. (After Greenwood and Crew.) C, a Brown Leghorn cockerel that acquired plumage resembling that of a female as a result of being fed desiccated thyroid. D, a hen-feathered Brown Leghorn male, the result of breeding. E, a cock-feathered Silver-Laced Wyandotte, male. F, a hen-feathered Silver-Laced Wyandotte male. (U. S. D. A.)

ıe began laying again and in the fall, molted and resumed female ıumage.

When the left ovary of a normal female is removed by operation, ıe rudimentary right gonad usually enlarges and produces pronounced ffects in certain directions. Therefore, in studies on the effects of the male gonads on plumage development, it has been found necessary remove the normal right ovary and the rudimentary right gonad, ı operation referred to as "bilateral ovariotomy."

A general review of the effects of bilateral ovariotomy is given by omm (1939). When bilateral ovariotomy is performed on an adult male belonging to either a hen-feathered or any other breed, she cquires the plumage characteristic of the capon, the ovariotomized male being called a poulard. When bilateral ovariotomy is performed, prior to the assumption of adult female plumage, the poulard evelops typical juvenile male plumage which is subsequently replaced y adult male plumage. The type of plumage developed following nistral ovariotomy, the removal of the left ovary but not the rudientary right gonad, varies considerably, depending upon the age at hich the female is operated upon. Sinistrally ovariotomized females ıat have acquired male-type plumage may later acquire female-type ıumage, because of the influence of secretions elaborated by the ılarged rudimentary right gonad.

When the ovary of a hen is transplanted into a capon, the capon-ype plumage reverts to the female type, as shown by Caridroit (1926) ıd Domm (1928), although Domm (1939) points out that such minized capons ultimately revert more or less completely to the ıpon type of plumage. Kopeć and Greenwood (1929) demonstrated ıat injections of egg yolk into sinistrally ovariotomized females ıused the capon type of plumage in the poulard to revert to the male type.

Bilaterally ovariotomized females into which have been transanted testicular grafts retained the male type of plumage characristic of the typical poulard, as shown by Domm (1929).

The results of these experiments demonstrate that the testicular ormone does not modify the male or female plumage of cock-feathered reeds and that the female hormone elaborated by the ovary suppresses ıale plumage. It has also been shown that when an adult female is nistrally ovariotomized, she acquires male-type plumage which subequently reverts to female-type plumage as a result of a female ormone elaborated by the hypertrophied rudimentary right gonad.

Skin Grafting and Plumage Development. When the castraon of a cock-feathered male is followed by the implantation of testes

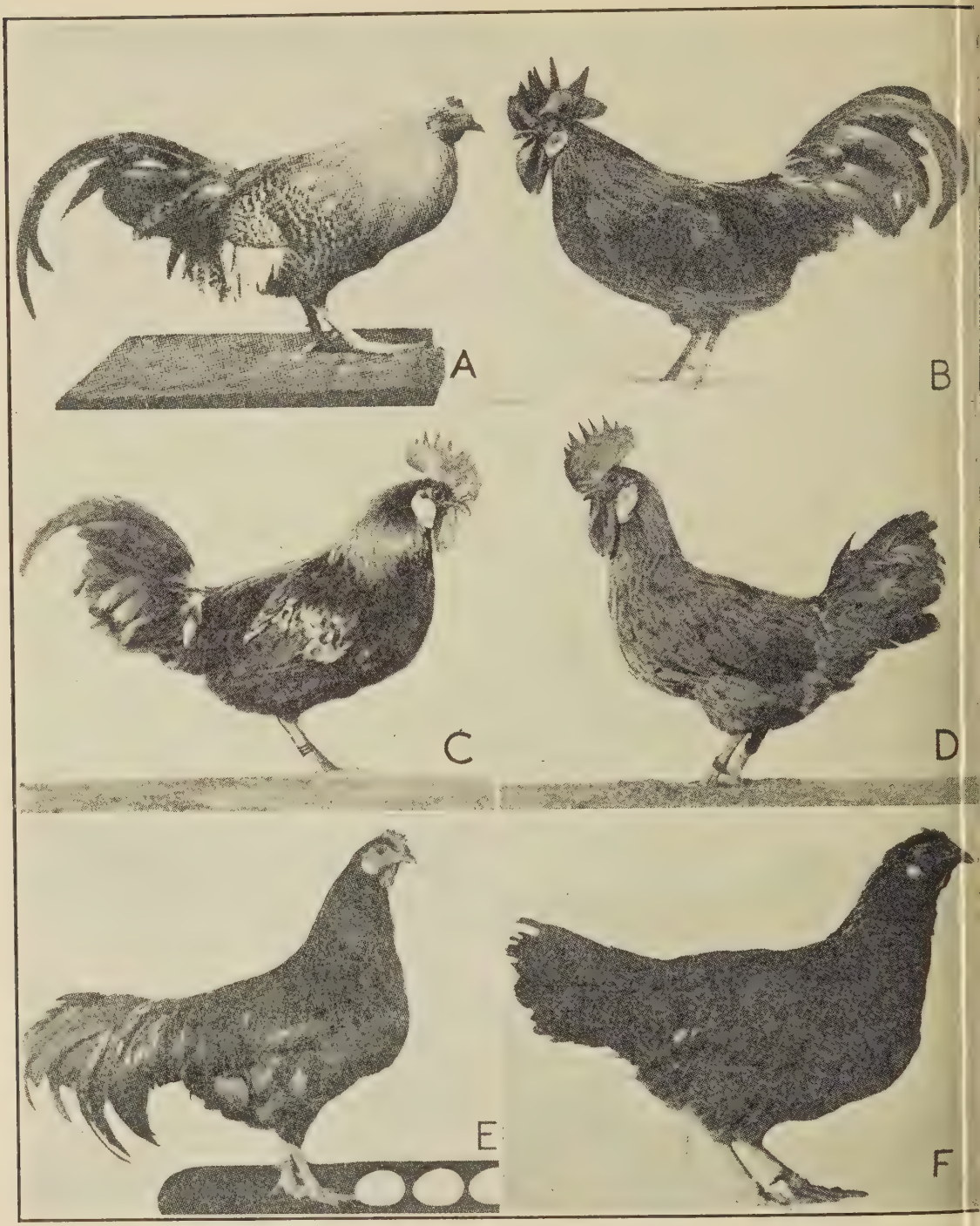

FIG. 12. Females sometimes look very much like males. A, a female that as
sumed male plumage and developed spurs, known as a developmental poular
(After Greenwood and Crew.) B, a female Brown Leghorn from which th
left ovary was removed at thirteen days of age, photographed two years later
she is known as a poulard. (After Domm.) C, a female Brown Leghorn whic
assumed male head furnishings and plumage and seven months later her plum
age returned to that of a female, as shown in D, although she retained mal
head furnishings. (After Greenwood and Crew.) E, a female that looked lik
a male but laid eggs and later acquired female plumage, as shown in F. (Afte
Cole.)

rom a hen-feathered male, there is no change in the type of plumage hat subsequently develops, the plumage maintaining its capon type as hown by Roxas (1926) and Greenwood (1928). When the castration f a hen-feathered male is followed by the implantation of testes from cock-feathered male, the capon type of plumage in the castrate everts to the female type, as shown by Roxas (1926). These results ould appear to indicate that the testes of cock-feathered and hen-eathered males differ with respect to their influence on plumage evelopment.

That such is not the case, however, is shown by the results secured rom experiments by Danforth and Foster (1927, 1929), Danforth 1930*a*), and Champy and Demay (1932) on grafting skins from ither sex of a cock-feathered breed onto either sex of a hen-feathered reed and vice versa. When the skin of a hen of a cock-feathered reed was grafted onto a hen of a hen-feathered breed, the feathers rowing from the grafted skin were of the female type. When the kin of a hen of a hen-feathered breed was grafted onto a hen of a ock-feathered breed, the feathers growing from the graft were also f the female type. When the skin of a hen of a hen-feathered breed as grafted onto a male of a cock-feathered breed, the grafted skin eathers were of the female type. Likewise, when the skin of a male f a hen-feathered breed was grafted onto a male of a cock-feathered reed, the grafted skin feathers were of the female type. However, hen the skin of a hen of a cock-feathered breed was grafted onto a ale of a cock-feathered breed, the grafted skin feathers were of the ale type, and, when the skin of a male of a cock-feathered breed was afted onto a male of a hen-feathered breed, the grafted skin feathers ere also of the male type.

From the results of these experiments, it appears that the differ-nce in plumage between the males of the cock-feathered and hen-athered breeds is owing to a difference in the reactivity of the skin ructures to the stimulus resulting from the presence of the gonad, as bserved by Greenwood and Blyth (1938). A factor for hen-feathering the hen-feathered breed is directly effective in the skin rather than rough the endocrine system, or, in other words, hen-feathering in n-feathered breeds, such as Campines and Sebright bantams, is due the genetic constitution of these breeds rather than to the influence hormones. Danforth (1937) observed that at the time of hatching, e potentialities of the definitive feather follicles are definitely termined.

The results of skin grafting experiments conducted by Danforth owed that when the skin of a Rhode Island Red male was grafted

FIG. 13. A, 6-day-old Barred Plymouth Rock chick with White Wyandotte head skin ectoderm taken from 72-hour embryo and grafted on the Barred Plymouth Rock embryo at 74-hour incubation. B, a 15-day-old Black Minorca chick to whose limb-bud base at 72-hour incubation was grafted skin ectoderm from head of White Silkie embryo; the feathers are white like the donor but their shape, structure, and rate of growth were controlled by the host. C, a 9-day-old White Leghorn chick with barred feathers in the right wing produced by grafting limb-bud mesoderm from 72-hour Barred Plymouth Rock embryo. D, 1-day-old White Leghorn chick with skin graft from Barred Plymouth Rock embryo. E same chick as D when 30 days old. F, same chick as D and E when 51 days old (Willier and Rawles.)

onto a White Leghorn hen, the feathers that grew from the graft were of female type. It was also shown that the skin of a Barred Plymouth Rock male grafted onto a Rhode Island Red female developed feathers that were female in type but barred, as far as pattern was concerned. Conversely, the skin of a Barred Plymouth Rock female grafted onto a Rhode Island Red male developed feathers that were of the male type but barred.

Willier, Rawles, and Hadorn (1937) performed ingenious experiments in grafting the skin of the embryo of one breed onto the embryo of another breed after seventy-five hours of incubation. The skin of Rhode Island Red embryos grafted onto White Leghorn embryos developed red down. The skin of embryos having black down grafted onto White Leghorn embryos developed black down. The skin of White Leghorn embryos failed to develop white down when grafted onto embryos having black down or onto Rhode Island Red embryos. The results show that when skin ectoderm from pigmented breeds is grafted onto unpigmented hosts, black or red pigment develops in accordance with the color of the host embryo. When unpigmented ectoderm is grafted onto pigmented host embryos, patches of white skin fail to appear. It appears, therefore, that the fate of the grafted skin is different in reciprocal graft-host combinations.

Willier and Rawles (1938*a*, 1938*b*) found that, after hatching, the down of the grafted areas is replaced by juvenile feathers having the characteristic form, rate of growth, and arrangement of the feather tracts or pterylae in corresponding positions in host controls. For instance, skin ectoderm taken from the dorsal-lateral surface of the head of a Barred Plymouth Rock embryo and grafted on the site of the wing-bud base of a White Leghorn embryo developed characteristic wing feathers, which were barred black and white. Conversely, when skin ectoderm taken from the wing bud of a White Leghorn embryo was grafted onto the dorsal surface of the head of a Barred Plymouth Rock embryo, the black and white barred feathers that grow from the graft were of the same length and shape as the white head feathers of the White Leghorn host. In no case did the feathers which were formed from implanted grafts bear any resemblance in shape or distribution to the feathers characteristic of the feather tract from which the graft was taken.

Moreover, it was found that the rate of growth of wing feathers arising from grafts is of the same order as the rate of growth of the wing feathers of the host. For instance, when the Barred Plymouth Rock, which is a slow-feathering breed, is the donor, the black and white barred wing feathers arising from a graft on the wing-bud base

of a White Leghorn, which is a rapid-feathering breed, grow at the same rate as the wing feathers of the opposite wing of the White Leghorn host.

Skin ectoderm of the Silkie breed, in which the barbicels are absent from the barbules, which are formed on each side of the barb of a feather, grafted onto Black Minorca and Barred Plymouth Rock gave rise to feathers similar to those of the host. It would appear that the feather germs of the epidermis of the host control feather structure.

Willier and Rawles (1938*b*) also found that ectoderm skin grafts interchanged among the White Leghorn, White Plymouth Rock, and White Wyandotte always produced white feathers. White Leghorn ectoderm skin grafts on Buff and White Minorcas developed white feathers.

Thus it appears that pigmented breeds differ when they serve as hosts to grafts of White Leghorn ectoderm. In the case of Buff and Black Minorcas, grafts of White Leghorn ectoderm develop white feathers, whereas in the case of Barred Plymouth Rocks and Rhode Island Reds, grafts of White Leghorn ectoderm develop colored feathers. In the latter case, the donor-controlled juvenile plumage of the graft is gradually replaced by adult plumage, which is of the same color as that of the host. Upon the attainment of sexual maturity, molting takes place, the new feathers being of the same color as that of the host.

The experiments on color control of the grafted areas were carried further by Watterson (1938), who found that grafts of a small piece of Barred Plymouth Rock limb-bud mesoderm, without the overlying ectoderm, implanted into the wing bud of a White Leghorn gave rise to donor-colored black down, the same as in the case of skin ectoderm grafts. Upon hatching, the black down gave rise to juvenile black and white barred feathers that had the shape and rate of growth characteristic of the White Leghorn host. White Leghorn wing-bud mesoderm grafted onto a Barred Plymouth Rock produced black down, which later gave rise to juvenile black and white barred feathers.

Thus, according to the results secured by Willier and Rawles (1938*b*), Rawles (1938), Watterson (1938), and Rawles and Willier (1939), the color-controlling factors reside in the skin of the host. In other words, pigment formation is predetermined in cells arising from nerve tissue. According to Danforth (1939), the pigmentation of feathers is determined largely by migratory pigmentoblast, which determines not only the color but also the feather pattern.

Eastlick (1939) made reciprocal limb-bud grafts between embryos of Brown and White Leghorns and observed considerable variability

in the characteristics of the donor tissue. Some of the donor tissue grafts resembled the host, some the donor, and others showed characteristics of both host and donor. Eastlick has suggested that the degree of attachment of the tissue determines whether an enzyme from the host reaches the graft and suppresses the color of the donor and stimulates the development of host pigment and plumage.

Hormones and Plumage Development. From the results of extensive experiments on gonadectomy, gonad transplantations, and skin grafting, it is quite apparent that the testes have little if any effect on the sexual character of the plumage, but that the ovary secretes a hormone which has a pronounced effect on feather structure and plumage pattern.

It is interesting to observe at this time that three cases have been reported of a change from normal colored plumage to white in the following three females: a Blue Andalusian reported by Lippincott (1920), a Black Leghorn reported by Crew (1922), and a Black Minorca reported by Goodearl (1939). The cause of the change in color has not been definitely established but in all probability involves an interference with the normal functioning of the ovary and the thyroid.

There is general agreement among the investigators that such characters as comb, voice, and behavior are affected by castration and are, therefore, dependent on male or androgenic hormones for their expression.

Apparently the testes have no influence on the sexual characters of the plumage, male-type plumage occurring in the castrates of both sexes. Male-type plumage is regarded, therefore, as being asexual or neutral. It should be noted, however, that Greenwood and Blyth (1938) observed certain Brown Leghorn males with some plumage of the female type and found that a ten-week-old Brown Leghorn male that had had relatively large amounts of testicular material introduced into the body cavity developed female feathering in the breast and saddle feathers. They suggested that the development of female-type feathers was due to the secretion of androgenic substances by the testes.

On the other hand, Juhn and Gustavson (1930*a*), Freud, de Jongh, and Laqueur (1930), Greenwood and Blyth (1935), and Parkes (1937) have demonstrated that the injection of a female sex hormone called "oestrin" into Brown Leghorn capons and poulards resulted in the development of female-type plumage. The response to oestrin among the feathers of different tracts is of the following order: back, saddle, breast, and tail. It has been pointed out previously that the rate of growth of the feathers of these four areas follows the same order. Juhn, Faulkner, and Gustavson (1931) observed a direct relationship

between growth rate of male feathers and the concentration of oestrin required to change the plumage from male type to female type in the Brown Leghorn capon.

The reversion of male-type plumage to female-type plumage involves not only a change in feather structure but also a change in color, the long and pointed hackle and saddle feathers of the capon and poulard being supplanted by shorter and rounded feathers with varying degrees of pigmentation. The black breast feathers of the Brown Leghorn capon are replaced by red or salmon colored feathers. Greenwood and Blyth (1935) observed that the replacement of black by red is of direct occurrence and suggested that oestrin exerts its influence by diffusion through the intervening tissues and not through the general circulation. Cook, Dodds, and Greenwood (1934) have shown that certain pure chemical compounds (1-keto-1, 2, 3, 4-tetrahydrophenanthrone and 9, 10-dihydroxy-9, 10-di-a-butyl-9, 10-dihydro-1, 2, 5, 6-dibenzanthracene) have the same biological activity qualitatively as the normal estrogenic hormones.

The sinistrally ovariotomized poulard, with its male-type plumage, reverts to female-type plumage owing to the production of oestrin as the result of the activation of the germinal epithelium of the testis-like right gonad, as demonstrated by Gray (1930).

In the normal female that has not been operated upon, the characteristic female-type plumage is due to the elaboration of the female sex hormone by the ovary.

That the female sex hormone elaborated by the ovary is not the only factor involved in the development of female-type plumage has been demonstrated by research on at least one of the other endocrine glands. Thyroxin, a hormone elaborated by the thyroid gland, exercises a pronounced effect on the structure and pigmentation of feathers. All the details of the various lines of research work cannot be entered into here, but sufficient of the general results are given to indicate the general role of thyroxin in the development of plumage.

Relatively heavy doses of thyroid fed to birds with colored plumage results in the depigmentation of the feathers as demonstrated by Giacomini (1924), B. Zavadowsky (1925) and Hutt (1930), the last investigator observing that daily doses of 4 milligrams thyroid iodine per 1,000 to 2,000 grams of body weight (about 2.5 to about 4.0 pounds) proved lethal to males and females and that the minimum daily dose necessary to produce marked depigmentation was 4 milligrams thyroid iodine to 5,000 grams of body weight. Martin (1929) showed that single doses, varying from 8 to 35 grams, of desiccated thyroid, caused a loosening of the feathers in from 3 to 10 days,

followed by a molt. Barbicels were absent on the barbs in the feathers but grew in immediately following thyroid feeding in larger than physiological doses.

On the other hand, Cole and Reid (1924), Crew (1925), and Torrey (1926) observed that the feeding of desiccated thyroid, when given in lesser amounts than those reported to produce depigmentation, resulted in the pigmentation in the feathers of cockerels and capons but not in those of hens. Moreover, the development of hen feathering in male fowls fed desiccated thyroid has been demonstrated by Torrey and Horning (1922, 1925) and Cole and Reid (1924). The development of hen feathering in males was also obtained by Cole and Hutt (1928) by feeding fresh thyroid gland and Armour's desiccated thyroid.

Greenwood and Blyth (1929) observed that hypothyroidism results in a diminution of the amount of melanic pigment in the feathers of the Brown Leghorn, a coincident increase in the amount of red pigment appearing in the feathers, and an increase in the amount of the fringing of the feathers due to lack of barbule formation. These authors also observed that hyperthyroidism in the male gives rise to an increase in the melanic pigment in the feathers while the red pigment and fringing tend to disappear. In the female, the effects of hyperthyroidism are slight.

Juhn and Barnes (1931) showed that the response in the feather germ to either thyroxin or thyroglobulin is roughly proportional to the dosage, the width of the pigmented area in the base of the feather germ deposited daily serving as an index of the circulating effective principle. Juhn and Fraps (1934) observed that barb frequency and barb length are modified by thyroxin over a considerable range anterior to the first barb that shows pigment deposition.

By administering graded doses of thyroid substance to mature cocks, Chu (1938) found that it was possible to reproduce plumages resembling those of the second and third juvenile generations. Similar treatment of six-week-old cockerels, from which the thyroid glands had been removed, resulted in the development of adult plumage. Chu has suggested that the sequence of juvenile and adult feather types exhibited by growing Brown Leghorn males expresses a gradually lessening degree of hyperthyroidism, owing to a gradual decrease in the level of thyroid activity or to changing levels of response in the feathers.

Crew (1926) removed the thyroids from the normally hen-feathered Campine male and observed an elongation of the saddle feathers and a restriction of barbules. Parkes and Selye (1937) removed the

thyroids from the Sebright bantam, another hen-feathered breed, and observed the development of male-type feathering.

Greenwood and Blyth (1934) have shown that when the thyroid was removed there was a diminution in the amount of melanic pigment formed and a coincident increase in the amount of red pigment and an increase in the amount of fringing. It was suggested that in the Brown Leghorn, the plumage typical of the male is developed independently of the gonad, but that the maintenance of typical male plumage is dependent upon a certain level of thyroid functioning.

Parkes and Selye (1937) removed the thyroids from birds of different breeds and observed the following results: (1) loss of barbules leading to fringing, (2) the elongation of feathers in relation to their width, (3) no pigment response in all-black breeds, (4) the black ventral feathers of Brown Leghorns changed to brown, (5) the black ventral feathers of Silver-Gray Dorkings changed to white, (6) the feathers of the Ancona lost their white tips.

In a general summarization of the influence of thyroxin, secreted by the thyroid gland, on the development of female plumage, Greenwood and Blyth (1938) point out that both ovary and thyroid play a part. The ovary stimulates the thyroid to a higher level of activity than prevails in the male or the capon, but at the same time, the ovary acts in opposition to the thyroid in restricting the deposition of melanic pigment. In the breast of the Brown Leghorn female, the deposition of melanic pigment is more or less completely inhibited and in the upper surface of the female, the melanic pigment is restricted to fine pencilings.

Hormones and Molting. The fact that capons start to molt earlier than normal males and that normal males begin molting earlier than persistent-laying females indicates that sexual activity is instrumental in inhibiting the onset of the molting process. The molting process, however, involves a complicated physiological mechanism in which other endocrine glands besides the sex glands play a part. It has been demonstrated that daily implantations of the anterior lobe of the pituitary gland in hens about to undergo the molting process resulted in a retardation of the onset of molting. The removal of the anterior lobe of the pituitary gland is followed by a rapid and extensive molt. It is not to be concluded, however, that the anterior lobe of the pituitary gland in itself inhibits the molt, for its removal invariably results in the degeneration of the sex glands. Moreover, the removal of the sex glands results in an increase in the size of the anterior lobe of the pituitary gland in both males and females. From this it might

be expected that the molting process in the capon would be retarded, whereas the onset of molting in capons takes place earlier than in normal males and much earlier than in persistent-laying hens. The reason that capons, without the sex glands but with an enlarged anterior lobe of the pituitary gland, start molting relatively early is because the anterior lobe of the pituitary secretes a hormone that stimulates the thyroid gland, which in turn secretes another hormone that induces molting.

In the case of laying hens, the onset of the molt is conditioned by the activity of the ovary and the anterior lobe of the pituitary gland, and, when these glands cease to function or function at a lower level, molting is induced through the activation of the thyroid gland. Molting in persistent layers takes place later than in nonpersistent layers as a result of heritable differences in the functioning ability of the ovary and the anterior lobe of the pituitary gland. There can be no doubt that persistence of production is inherited, for by the adoption of a proper system of selection and breeding it is possible to develop in a flock persistent production to a relatively high degree.

That laying and molting are two separate processes controlled by different mechanisms, with secondary actions between the two, has been proposed by Van der Meulen (1939).

Gynandromorphic Plumage. Female- and male-type plumage occurring simultaneously in the same bird is spoken of as gynandromorphism and is encountered occasionally. As a matter of fact, there are often feathers on a bird in which a relatively sharp transverse division occurs in each feather between the male and female parts. The feather may have a male tip and a female base or the reverse. Such feathers can be produced experimentally by intermittent injections of oestrin into capons. Feather pattern may be modified in hackle and saddle feathers by injections of thyroxin at properly spaced intervals.

Domm (1927) found that when a poulard with its male-type plumage reverted to female-type plumage, due to the estrogen secreted by the hypertrophied right gonad, the back and saddle feathers were the first to change, followed by the breast and lateral feathers. Juhn and Gustavson (1930) demonstrated that as the result of intermittent injections of estrogen into capons, the regenerating breast feathers recorded the interruption by a temporary reversion to male type, whereas growing saddle feathers remained female in type. The saddle feathers apparently had a lower threshold of response to estrogen than the breast feathers. Juhn, Faulkner, and Gustavson (1931) demon-

strated a relationship between growth rate of male feathers and the concentration of estrogen required to change the type of growing feathers from male type to female type.

Lamoreux (1939) injected a female sex hormone, Progynon B, twice daily over a period of sixty days into F_1 males that were produced by a mating of a Barred Plymouth Rock male with Silver-Spangled Hamburg females after all feathers had been plucked except the remiges from the right side of the bodies. The new feathers, grown under the influence of the female sex hormone, were of female type and barred, whereas the left side retained its male-type plumage, and hackle, saddle, and wing feathers remained irregularly white and spangled just as the right side before being plucked. The pseudo-gynandromorph plumage condition of these birds effectively illustrates the influence of female sex hormone upon both the color and structure of feathers which have the same genetic constitution.

TABLE 4. SHOWING THE TYPE OF PLUMAGE, ♂ OR ♀, FROM THE STANDPOINT OF FEATHER FORM AND STRUCTURE ONLY, THAT DEVELOPS UNDER A GIVEN SET OF CONDITIONS IN A MALE (♂) AND A FEMALE (♀) BELONGING TO COCK-FEATHERED (C. F.) AND HEN-FEATHERED (H. F.) BREEDS, NO DISTINCTION BEING MADE BETWEEN CAPON AND NORMAL COCK PLUMAGE

	Type of Plumage
♂ of C. F. breed—testes	= ♂
♂ of H. F. breed—testes	= ♂
♀ of C. F. breed—ovary	= ♂
♀ of H. F. breed—ovary	= ♂
♀ of C. F. breed—ovary[1] + testicular implants of C. F. breed	= ♂
♂ of C. F. breed, with testes + testicular implants of H. F. breed	= ♂
♂ of C. F. breed—testes + testicular implants of C. F. breed	= ♂
♂ of C. F. breed—testes + testicular implants of H. F. breed	= ♂
♂ of H. F. breed—testes + testicular implants of C. F. breed	= ♀
♂ of C. F. breed—testes + ovary implant	= ♀[2]
Skin of ♂ of C. F. breed grafted onto ♂ of H. F. breed	= ♂
Skin of ♀ of C. F. breed grafted onto ♂ of C. F. breed	= ♂
Skin of ♀ of C. F. breed grafted onto ♀ of H. F. breed	= ♀
Skin of ♂ of H. F. breed grafted onto ♂ of C. F. breed	= ♀
Skin of ♀ of H. F. breed grafted onto ♀ of C. F. breed	= ♀
Skin of ♀ of H. F. breed grafted onto ♂ of C. F. breed	= ♀
♂ of H. F. breed—testes + androsterone	= ♂
♂ of H. F. breed—testes + estrone	= ♀
♂ of H. F. breed—testes + testosterone	= ♀
♂ of H. F. breed—testes + androstenedione	= ♀
♂ of C. F. breed—testes + thyroid feeding	= ♀
♂ of C. F. breed—thyroids	= ♂

[1] Bilaterally ovariotomized.

[2] When bird molts.

Other Endocrine Gland Effects. From what has been said previously, it would appear that the endocrine glands chiefly responsible for changes in the various secondary sexual characters are the gonads, pituitary, and thyroids. Little work has been done with the other endocrine glands, although some of them apparently are of tremendous importance in avian physiology.

Investigating the effects of the removal of the adrenals on the sex characters of the fowl, Parkes and Selye (1936) observed that the operation, if successful, was fatal. However, in the case of a Sebright bantam male from which most of the adrenal was removed, it was observed that new feathers, growing in to replace ones that had been plucked at the time of the operation, showed the tips of the feathers to be of the capon type. Herrick and Torstveit (1938) found that, after the adrenals had been removed from White Leghorn males and cortical hormone injected, the combs took on the appearance of a capon and the testes degenerated.

In experiments on the removal of the pineal gland, Foa (1914) reported that a precocious development of the secondary sexual characters took place in males but not in females. Izawa (1923) observed an increase in the size of the comb and an increase in body weight. Kozelka (1933*b*) concluded, however, that the removal of the pineal gland produced no significant changes.

Greenwood (1931) observed that the thymus gland in sexually mature males was considerably greater in amount than in females. As orchotomy and ovariotomy cause a delay in the involution of the thymus, Greenwood finally suggests that a relationship exists between gonad and thymus involution. The results secured by Křiženecký and Nevalonnyj (1929) on feeding thyroid and thymus to Brown Leghorn chicks led them to conclude that the intensity of the feathering process is governed by the combined action of the thyroid and the thymus.

SEX REVERSAL

Since it has already been shown that as far as external appearances are concerned, females may look like males and still lay eggs and males may look like females, the question remains as to whether or not the sexes may be reversed. The problem has been studied most intensely during the past few years, and with the aid of hormones injected into developing eggs some very interesting results have been secured.

Female Sex Reversal. The presence of the left ovary in the female suppresses the development of the gonad on the right side, for,

when the left ovary is removed, the right gonad increases in size. Domm (1929, 1930) has shown that, if ovariotomy is performed on females within thirty days after being hatched, the hypertrophied right gonad may, in a few cases, contain male germ cells in varying stages of development. Padoa (1934) observed, however, that spermatogenesis may occur as frequently in birds ovariotomized between 3 and 6 months of age as in birds ovariotomized between 18 and 23 days of age.

The important point to be kept in mind is that the development of the male germ cells in the right hypertrophied gonad of ovariotomized females apparently proceeds from surviving primordial germ cells, according to the observations made by Benoit (1923*b*), Zavadowsky (1926), Padoa (1934), and Miller (1938). Apparently spermatogenesis occurs in tubules of medullary origin in which germ cells become incorporated. On the other hand, ovogenesis occurs when the primordial germ cells are incorporated in the cortex of the hypertrophied right gonad. From the medulla, male hormones are secreted; from the cortex, female hormones are secreted. The left ovary has a highly differentiated cortex. Otherwise, the left ovary produces the same hormone effects as the rudimentary right gonad. If the cortex of the left ovary is removed, the medulla of the left ovary may develop into a sterile testis-like organ. Domm (1931*a*) demonstrated that this testis-like left organ and the testis-like organ in the right rudimentary gonad of the ovariotomized female have the same endocrine potentialities.

Normal-appearing motile spermatozoa, obtained from poulards whose rudimentary right gonads had developed into testes, were injected into virgin females by means of artificial insemination, but the eggs laid by the virgin females were infertile.

The observation of Crew (1923) that complete sex reversal occurred in a Buff Orpington female so that it became a functional male was among the first of such observations to be made. It is unfortunate, however, that more definite information was not available concerning the early life history of the bird. It has been pointed out previously that embryos show no sexual differentiation prior to about six and one-half days of incubation. By injecting the albumen of eggs at forty-eight hours of incubation with male hormone preparations obtained from male human urine and bull testes, Willier, Gallagher, and Koch (1935, 1937) showed that the male urinary hormones produced a hypertrophy of the potential vasa deferentia in female embryos and inhibited the development of the oviducts, whereas the testes hormones produced no changes except a hypertrophy of the

Wolffian ducts of the female embryos. The urinary preparations contained androsterone and dehydroandrosterone, whereas the bull testes preparation contained testosterone.

Willier, Rawles, and Koch (1938) have shown that these three male hormone preparations, when injected into eggs incubated from 43 to 72 hours, effect certain changes in the gonads of genetic females, depending upon the dosage. With low dosages, the left ovary is not affected, but the right ovary enlarges, owing to the hypertrophy of the medullary tissue, and tends to assume a testis-like shape. Dosages exceeding 1.0 milligram usually effect a hypertrophy of the medulla of the left ovary and of the right ovary. Both ovaries assume the appearance of testes, the extent of the modifications in structure induced varying considerably. Thus, different grades of intersexuality are produced. Androsterone and dehydroandrosterone seem to be equally effective in their masculinizing effects, whereas higher concentrations of testosterone are required to produce similar modifications. Wolff and Wolff (1937) have shown that acetate of testosterone is quantitatively less effective in producing masculinizing effects in female Leghorn embryos than in embryos obtained from a cross of Rhode Island Red males mated to Light Sussex females.

The results secured from numerous lines of investigational work indicate that the female fowl is a hermaphrodite with respect to its endocrine organization and has the potentiality for forming a complete male genital system.

Male Sex Reversal. Insofar as known only a few cases have been reported in the literature of a complete reversal from male to female. Several cases have been reported, of course, in which males have spontaneously assumed the appearance of females as far as the secondary sexual characters are concerned. In most of these cases, the change in sexual appearance has resulted from the degeneration of the testes due to a tumor or other diseased condition.

On the other hand, the results secured by Dantchakoff (1936), Willier, Gallagher, and Koch (1935, 1937), Willier, Rawles, and Koch (1938), and Domm (1938) show that the genetic male possesses the potentialities for forming cortical tissue following the injection of female sex hormones. In the male embryo, the left testis passes through a stage during the early period of sexual differentiation when germinal epithelium containing germ cells is present on the surface of the gonad. This germinal epithelium may be stimulated to develop into ovarian cortex by the injection of oestrin during the second and third days of incubation.

Willier, Gallagher, and Koch (1937) injected theelin and theelol

into eggs at forty-eight hours of incubation and found that the left testis developed into a flattened ovary-like body consisting of both ovarian and testicular tissues, in two cases the left gonad being indistinguishable from a normal left ovary. The right testis remained relatively unchanged but oviducts persisted either partially or completely. The activation by the female sex hormone of the incipient ovarian cortex of the left testis is regarded as the first step in the process of sex reversal.

Domm (1938) injected eggs with oestrin during the second to fourth day of incubation and allowed the chicks to hatch and grow to maturity. The males exhibited a curious combination of male and female characters, the adult plumage varying from male type in some to almost completely female type in others. The type of plumage was found to be correlated with the structural components of the gonads. Post-mortem examination showed that the left testis had invariably undergone a reduction in size and had become ovary-like in appearance. This ovary-like gonad was found to be an ovotestis with a surface cortex. Underneath it were typical testis tubules in complete spermatogenesis. In some cases, oviducts were absent, whereas, in others, the oviducts were in various stages of development, the left oviduct usually being larger than the right one and sometimes being entirely normal. The right testis was found to be typically testicular, cortical tissue rarely being present.

Dual Potentiality of the Sexes. The results secured from the numerous investigations on the transformations that take place in the gonads and the secondary sexual characters indicate a certain dual potentiality of the sexes. The left ovary of the normal female has been shown to possess a cortex, which secretes a female sex hormone, and a medulla, which secretes a male sex hormone. The female sex hormone is largely responsible for the appearance of female-type plumage. When the left ovary is removed or is sufficiently affected by a tumor or is otherwise diseased, the right rudimentary gonad enlarges into a testis-like structure containing both cortical and medullary tissue, and the female-type plumage reverts to male-type plumage. The development of male-type head furnishings in either sex is due largely to the effects of male sex hormones.

The left ovary and the right rudimentary gonad of the female can produce either male or female morphohormones under certain conditions. Each of these gonads may also produce a typical testicular structure, spermatogensis not infrequently occurring in the hypertrophied right gonad. In the female, the head furnishings, spurs,

plumage, and Wolffian ducts retain the capacity to react to the male sex hormone as do the corresponding characters in the normal male. Likewise, these same characters in the male react to female sex hormones in the same manner as in the normal female. Thus it appears that the somatic tissues, as distinguished from germ tissue, may react to either male or female sex hormone equally in both sexes.

The bisexuality of the left testis has not only been demonstrated, but it has also been shown that ovarian cortex may develop in both the right and left testes.

On the other hand, evidence has been submitted showing that certain differences that exist between the sexes are not due to the gonads, and it has also been shown that the reactions of the somatic tissue to sex hormones sometimes differ in the two sexes. Furthermore, although it has been demonstrated that sexual differentiation depends upon a balance of action between the cortical and medullary tissues, the cortex giving rise to femaleness and the medulla to maleness, the potentiality of the undifferentiated embryo to develop into a male or female depends apparently upon the genetic constitution of the reproductive cell that gives rise to the embryo, a problem that is discussed more fully in the next chapter.

THE SEX RATIO

The discussion in the preceding sections of this chapter indicates that, under certain given conditions, the sex of a bird may be completely reversed, at least as far as anatomical structure is concerned. Nevertheless, existing knowledge concerning the various physiological factors involved in sex modifications make it readily apparent that under natural conditions complete functional sex reversal rarely, if ever, takes place.

Studies on the sex ratio of the domestic fowl are of interest from the standpoint of ascertaining the normal sex ratio and the extent and causes of any deviations therefrom. A determination of the cause or causes of any deviation from the normal sex ratio might lead to the possibility of modifying it as the result of breeding practice. First, however, it is necessary to determine the normal sex ratio, meaning the percentage of males of the total population.

From the extensive series of observations on the sex ratio of various breeds, given in Table 5, it is apparent that in the majority of cases there were slightly fewer males than females at the time the observations were made.

That large eggs tend to produce male chicks and that small eggs

TABLE 5. SEX RATIOS IN DIFFERENT STRAINS OF DOMESTIC FOWL OBSERVED BY VARIOUS INVESTIGATORS

Investigator	Year	Number of Observations	Sex Ratio
Darwin	1874	1,001	48.65 ± 1.06
Field	1901	2,105	44.63 ± 0.73
Thomsen	1911	805	47.82 ± 1.19
Pearl[1]	1917	20,037	48.57 ± 0.28
Pearl[2]	1917	22,791	49.45 ± 0.22
Crew and Huxley	1923	763	48.62 ± 1.21
Jull[3]	1924	936	48.82 ± 0.80
Jull[4]	1924	2,396	48.41 ± 0.47
Mussehl	1924	1,514	52.25 ± 0.87
Lambert and Knox	1926	2,910	51.13 ± 0.62
Horn	1927	2,131	51.62 ± 0.73
Lambert and Curtis	1929	2,510	46.82 ± 0.67
Callenbach	1929	7,859	49.41 ± 0.45
Christie and Wreidt[5]	1930	3,680	49.60 ± 0.82
Landauer and Landauer[6]	1931	5,683	52.70 ± 0.45
Byerly and Jull[7]	1935	17,989	47.56 ± 0.25
Byerly and Jull[8]	1935	28,015	50.10 ± 0.23
Byerly and Jull[9]	1935	7,997	52.60 ± 0.38
Byerly and Jull[10]	1935	9,444	48.40 ± 0.34
Byerly and Jull[11]	1935	4,800	50.80 ± 0.49
Byerly and Jull[12]	1935	23,125	50.00 ± 0.25

[1] Families of 10 or more chicks per family.
[2] Families of all sizes.
[3] Families of 10 or more chicks per family, produced in the normal hatching season.
[4] Families of 10 or more chicks per family, produced during the dams' first year of egg production.
[5] Standard error.
[6] Chicks that died up to two months of age.
[7] Embryos that died between ninth day of incubation and hatching time.
[8] Chicks of various breeds at 10 weeks of age.
[9] Rhode Island Red chicks at 10 weeks of age.
[10] White Leghorn chicks at 10 weeks of age.
[11] Families of chicks of various breeds in which there was no postnatal mortality up to 10 weeks.
[12] Families of chicks of various breeds in which there was some postnatal mortality up to 10 weeks.

tend to produce female chicks was claimed by Lienhart (1919), but the observations of Jull (1924) and Jull and Quinn (1924, 1925) show quite definitely that egg weight bears no relation to sex ratio. Jull and Quinn (1925) found no significant difference between the weights of male and female chicks at hatching time and Jull and Heywang (1930) found that the ratio of chick weight to initial egg weight is independent of the sex of the chick. Jull and Quinn (1924) also found that there is no relationship between the sex of the chick and the absolute length or the relative length or the shape of the egg from which the chick is hatched.

Jull (1924) showed that there is no relationship between yolk weight of egg and sex nor between yolk water content of egg and sex, and Jull and Heywang (1930) found that the ratio of yolk weight to chick weight at hatching time is independent of the sex of the chick.

The results secured by Mussehl (1924), Lambert and Curtis (1929), Callenbach (1929), Christie and Wreidt (1930), and Jull (1931*b*) show no relationship between antecedent egg production and sex ratio.

Lambert and Curtis (1929) and Christie and Wreidt (1930) observed no significant differences among the sex ratios of hens of different ages.

Callenbach (1929) secured results indicating that different strains of domestic fowl produce different sex ratios. Mussehl (1924) secured results that showed sex ratios of chicks from different males differed significantly, and Jull (1924) observed sex ratios of 91.67 and 66.67, respectively, among the chicks from two hens based on their total first-year egg production. Christie and Wreidt (1930) observed that some of their hens gave aberrant sex ratios. Jull (1931*b*) found that close inbreeding had no effect on the sex ratios of progenies produced and Jull (1932) showed that the tendency to produce a preponderance of either sex is not inherited.

That prenatal mortality does not affect the sex ratio has been determined by Thomsen (1911), Pearl (1917*a*), Crew and Huxley (1923), Jull (1924), Lambert and Knox (1926), Horn (1927), Lambert and Curtis (1929), and Byerly and Jull (1935).

Since prenatal mortality does not affect the sex ratio, it would naturally be expected that postnatal mortality between the sexes would not differ significantly. Landauer and Landauer (1931) found, however, as indicated in Table 5, that up to the end of the second month, the mortality of males exceeded that of females. On the other hand, Byerly and Jull (1935) observed no significant relation between hatchability of eggs and viability of chicks and, further, that when differential embryonic mortality between the sexes exists it is the female that shows the greater mortality.

The total number of individual observations in the various population, avoiding duplicates given in Table 5, is 102,143 and the sex ratio of the population comprising these different individuals 49.38 ± 0.16. If it be assumed that the primary sex ratio is 50, it is interesting to observe that the apparent normal sex ratio in the domestic fowl deviates slightly below 50 in contrast with a slight deviation above 50 in mammals whose genetic sex constitution is the reverse of that in birds.

PROBLEMS

1. What are the primary sexual characters and how do they function?
2. What are the chief differences between the sexes in respect to secondary sexual characters?
3. What are the more important steps involved in the formation of the egg?
4. What is the relationship between the component parts of the egg and the development of the embryo?
5. What is the relationship between the gonads and the development of the comb, wattles, and spurs?
6. (*a*) What are the more important changes that take place when a male is castrated?

(*b*) What are the more important changes that take place when the ovary of a female is removed?

(*c*) What are hen-feathered males, and what factors are responsible for the kind of feathering they have?

7. What are hormones and what is the difference in the effects produced in secondary sexual characters by male and female hormones?
8. What are the more important steps involved in the transformation of a male into an anatomical female and a female into an anatomical male?
9. What is the difference between sex differentiation and sex determination?
10. Discuss the role of hormones with respect to sex differentiation and sex determination.

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CHAPTER III

THE MECHANISM OF INHERITANCE

In the preceding chapter it has been pointed out that the secondary sexual characters and the gonads of the domestic fowl are subject to certain mechanisms of control involving the hormones elaborated by the glands of the endocrine system. It is obvious that sexual differentiation has a primary function with respect to reproduction, sex, and other characters appearing in a certain order of succession from the time that sexual differentiation first manifests itself in the developing embryo between six and seven days of age. Sexual differentiation is a consequence of sex determination, the latter phenomenon involving the factor or factors that are responsible for an embryo developing into a male or into a female. By sex determination is meant the primary determining constitution established in the fertilized egg, as the result of which the embryo develops either into a male or a female.

How Fertilization Takes Place. The mating of a male and a female serves the purpose of allowing the male and female reproductive cells to unite, for only in this way can a chicken be produced. The reproductive cells of the male are called spermatozoa; those of the female are called ova. The fertilization of an ovum or egg of the female is accomplished by its union with a spermatozoon. According to Lillie (1919), only one spermatozoon fertilizes the ovum, although several spermatozoa may be present in the semen surrounding the ovum. At the time of copulation the copulatory organ of the male ejects semen containing spermatozoa into the cloaca of the female, and the spermatozoa then traverse the length of the oviduct. Apparently each ovum is fertilized shortly after it enters the oviduct.

Gametes and Zygotes. From the standpoint of reproduction and the inheritance of characters, the reproductive cells are spoken of as "gametes," the term "gamete" meaning a spouse. The ovum is the female gamete and the spermatozoon is the male gamete. The fertilization of the female gamete by the male gamete produces the fertilized egg, which is spoken of as the "zygote," a term meaning yoked together. It is the zygote that develops into the chick.

Chromosomes. Each gamete contains little thread-like bodies called "chromosomes," which are transmitted from parent to offspring.

A fact of fundamental importance is that the number of chromosomes in any given species of animal is constant, as suggested by Agar (1920). The number of chromosomes in the chicken has been studied by Guyer (1916), Shiwago (1924), Hance (1924 and 1926), Akkeringa (1927), Suzuki (1930), White (1932), Sokolow and Trofimov (1933), Sokolow, Tiniakow, and Trofimov (1936), Popoff (1933), and Miller (1938), several of whom observed a relatively large number, a few being large and several very small. The evidence indicates that the chicken has at least 35 or 36 chromosomes but probably more.

Sex Chromosomes and Autosomes. The difference between the number of chromosomes in the male and the female is due to the fact that the male has one more sex chromosome than the female. The

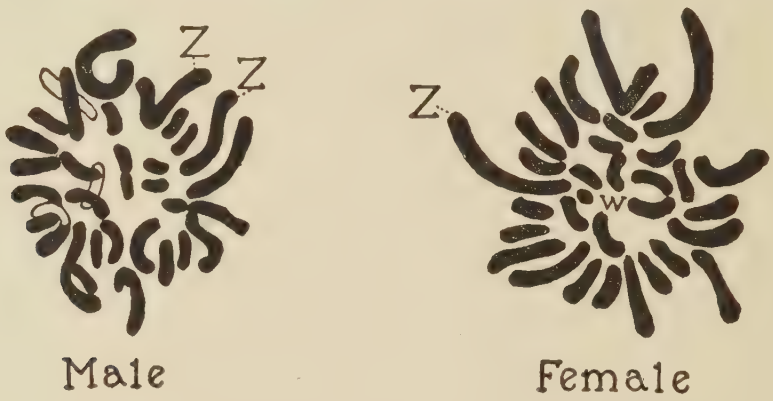

FIG. 14. The male and female chromosome groups of the domestic fowl (After Shiwago.) The chromosomes are contained in the nucleus of the reproductive cell and are always in pairs, except for the single sex chromosome in the female. Each chromosome is made up of a large number of tiny bodies, called genes, which are the units that give rise to the numerous hereditary characters of the fowl.

sex chromosomes in any species are apparently always associated with sex and may be a factor in its determination, hence their name. The rest of the chromosomes are called "autosomes," or ordinary chromosomes, and are always in pairs. The male chicken has at least 17 pairs of autosomes and 2 sex chromosomes, whereas the female chicken also has at least 17 pairs of autosomes but only 1 sex chromosome.

Sex Inheritance. It has been pointed out previously that the zygote is the result of the union of the male and female gamete, and it has also been stated that it is the zygote that develops into the mature chicken. Regardless of the actual number of autosomes there are, the fundamental principles of sex inheritance are not affected and may be illustrated by assuming that in both male and female there are 17 pairs of autosomes.

If the male chicken has 17 pairs of autosomes and 2 sex chromosomes, it is obvious that the two gametes which united to produce the

zygote that developed into a male must each have contained 17 autosomes and 1 sex chromosome. Perhaps an equation would make the matter clear: Male gamete with 17 autosomes and 1 sex chromosome + female gamete with 17 autosomes and 1 sex chromosome = a zygote with 17 pairs of autosomes and 2 sex chromosomes.

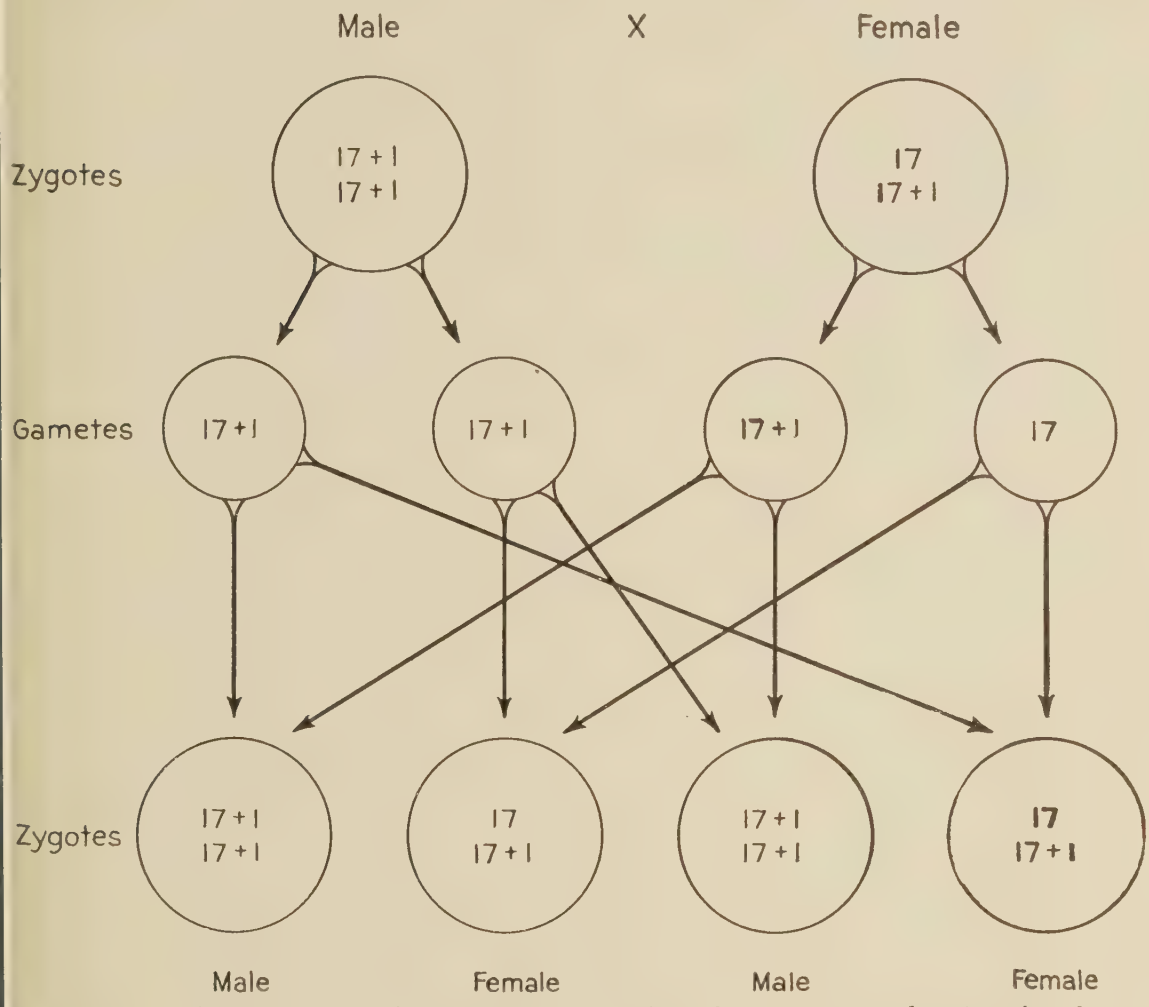

FIG. 15. The male fowl has at least 17 pairs of autosomes plus 1 pair of sex chromosomes, whereas the female fowl has at least 17 pairs of autosomes but only 1 sex chromosome. The male produces but one kind of gametes, each of which contains 17 autosomes plus 1 sex chromosome. The female produces two kinds of gametes, one kind containing 17 autosomes plus 1 sex chromosome and the other containing 17 autosomes but no sex chromosome. A male gamete uniting with a female gamete containing 17 autosomes plus 1 sex chromosome produces a zygote containing 17 pairs of autosomes plus 1 pair of sex chromosomes; such a zygote develops into a male. A male gamete upon uniting with a female gamete containing 17 autosomes but no sex chromosome produces a zygote containing 17 pairs of autosomes but only 1 sex chromosome; such a zygote develops into a female.

If the female chicken has 17 pairs of autosomes and 1 sex chromosome, it is obvious that, of the two gametes uniting to form the zygote, one must have had 17 autosomes and 1 sex chromosome and the other must have had 17 autosomes only. In the form of an equation the

situation is thus: A gamete with 17 autosomes and 1 sex chromosome + a gamete with 17 autosomes = a zygote with 17 pairs of autosomes and 1 sex chromosome.

Up to the present only one phase of the reproductive cycle has been discussed, the union of a gamete of paternal origin with a gamete of maternal origin. The other phase of the reproductive cycle consists in the development of the gametes from the zygotes. For the sake of simplicity, the behavior of the sex chromosomes in the processes involved is omitted from this brief discussion. Each zygote gives rise to numerous germ cells. The chromosomes in each germ cell unite in pairs, a particular chromosome of paternal origin pairing with a similar chromosome of maternal origin. The chromosomes then split lengthwise twice. After the second splitting is completed, the germ cell divides, half of the chromosomes going into one cell and half into the other; each cell contains, therefore, half as many chromosomes as the germ cell. These cells, each containing the half number of chromosomes, are called gametes. A gamete of male origin upon uniting with a gamete of female origin gives rise to the formation of a zygote, which contains the full complement of chromosomes depending upon the sex of the zygote. The female is spoken of as being heterogametic, since the female zygote gives rise to unlike gametes with respect to the sex chromosome.

A very important point always to be kept clearly in mind is that when the gamete of female origin containing the sex chromosome unites with a gamete of male origin, the zygote produced is a male, whereas when the gamete of female origin that does not contain the sex chromosome unites with a gamete of male origin, the zygote produced is a female. Another fundamental point always to be kept clearly in mind is that either of the unlike gametes of female origin may mate with either of the like male gametes.

Genes Give Rise to Characters. The chromosomes are the bearers of the determiners of the hereditary characters, but, since there are hundreds of characters and only about 17 pairs of autosomes and 1 or 2 sex chromosomes according to the sex, it is obvious that each chromosome must be responsible for the development of many characters. Each chromosome is made up of smaller units called "factors" or "genes." It is the genes that give rise in development to such characters as plumage color, lacing, penciling, spangling, barring, single comb, rose comb, feathered shanks, yellow shanks, hatchability, and egg production.

SEX-LINKED INHERITANCE

Many characters which fowls possess are inherited equally from sire and dam. The genes giving rise to such characters are borne on the 17 or more pairs of autosomes common to both sexes, half of the chromosomes being of maternal and half of paternal origin in the case of any individual fowl.

There are certain characters, however, that are transmitted from dam to son but not from dam to daughter, although they are transmitted from sire to both son and daughter. Characters transmitted from dam to son only are called "sex-linked" characters because it is reasonably certain that the genes that give rise to such characters are borne on the sex chromosomes.

The fact that certain characters are inherited on a sex-linked basis is easy to understand when one keeps in mind the difference between the male and female chicken in respect to the number of sex chromosomes each possess.

It will be recalled that the male chicken has 2 sex chromosomes, whereas the female has only 1. In the case of the chicken the inheritance of sex is commonly referred to as the *WZ* type because the symbol *Z* is used to denote the presence and *W* the absence of one of the pair of the sex chromosomes. Every male zygote has 2 sex chromosomes (*ZZ*), so that among all male gametes produced each contains one *Z* chromosome. Every female zygote has only 1 sex chromosome (*Z*), and it produces gametes in approximate equality with and without the *Z* chromosome, a gamete with the *Z* chromosome being called a *Z* gamete and one without the *Z* chromosome being called a *W* gamete. Sex-linked genes, being borne on the sex chromosome only, are contained in the *Z* gametes only, the *W* gamete having no sex chromosome and, therefore, containing no sex-linked genes.

The female fowl is heterozygous (from *heteros*, meaning different, and *zugon*, referring to the condition of the zygote, *WZ*) for sex because she has only 1 sex chromosome, whereas the male is homozygous (from *homo* meaning alike, and *zugon*, referring to the condition of the zygote, *ZZ*) because he has 2 sex chromosomes. The gene for barring, being sex-linked, is borne on the sex chromosome *Z*.

The *WZ* type of sex inheritance is common to birds, moths, and butterflies, but in many other animals another type of sex inheritance occurs. It is called the *XY* type of sex inheritance, in which the male is heterozygous for sex because he has only 1 sex chromosome (*X*) and the female is homozygous for sex because she has 2 similar sex chromosomes, known as *X* and *X*. As far as sex is concerned, the

female zygote contains X and X chromosomes and produces gametes each having an X chromosome, whereas the male zygote, which con-

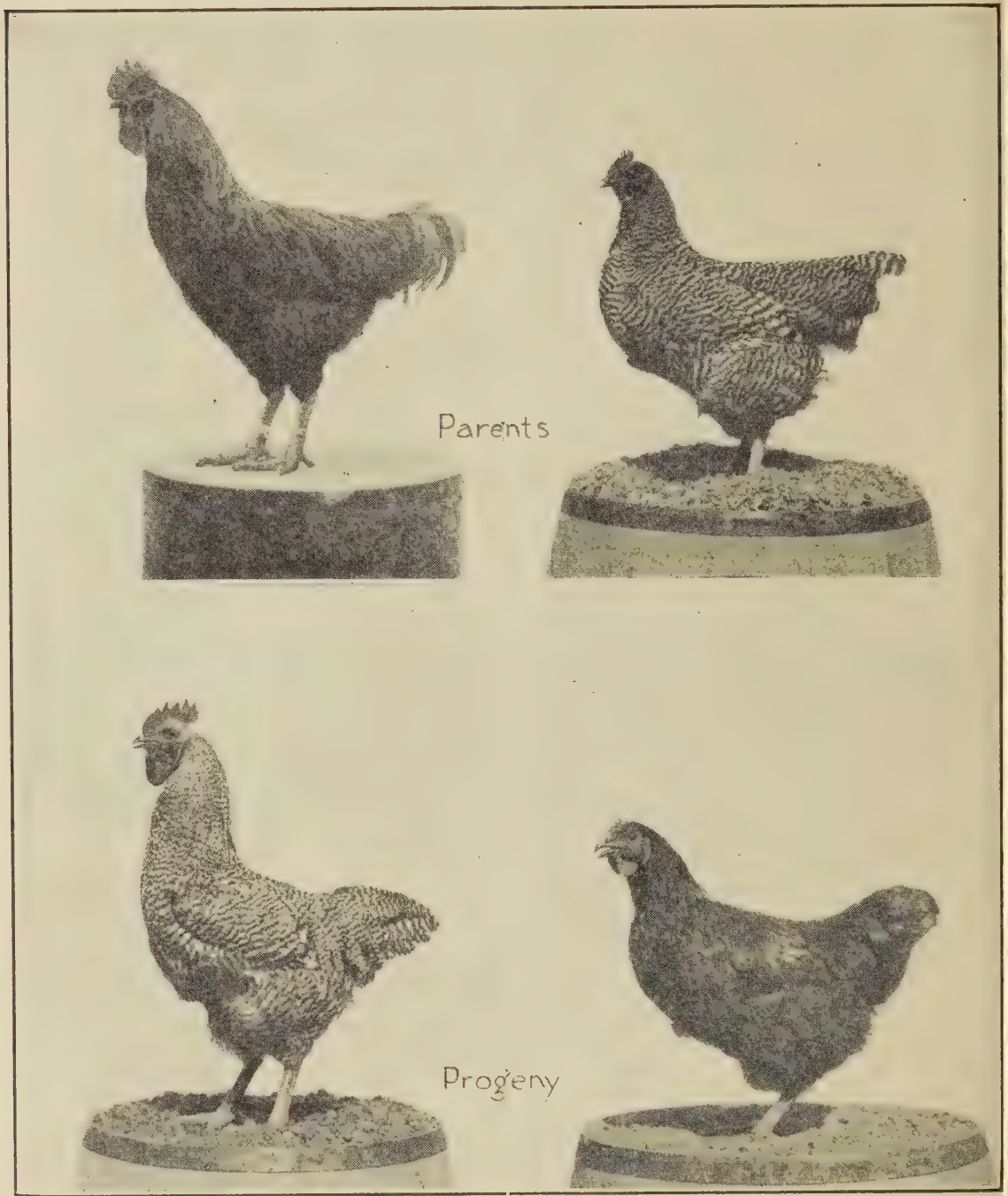

FIG. 16. Illustrating the inheritance of a sex-linked dominant character. The gene for barring in Barred Plymouth Rocks is contained in the sex chromosome and when a Barred Plymouth Rock female is mated to a nonbarred colored male, such as Rhode Island Red, the gene for barring is transmitted to the sons only. The manner in which this is accomplished is shown in Fig. 18. The daughters are black, sometimes with a reddish tinge on the head, neck or breast. The daughters are nonbarred because each one received its sex chromosome from the nonbarred sire, as shown in Fig. 18. (U. S. D. A.)

tains but 1 X chromosome, produces two kinds of gametes in approximate equality, one gamete containing an X chromosome for every one

ithout it, the latter being known as the *Y* gamete. The difference etween the *WZ* and *XY* types of sex inheritance is that in the *WZ* ype the male is homozygous for sex chromosomes and consequently

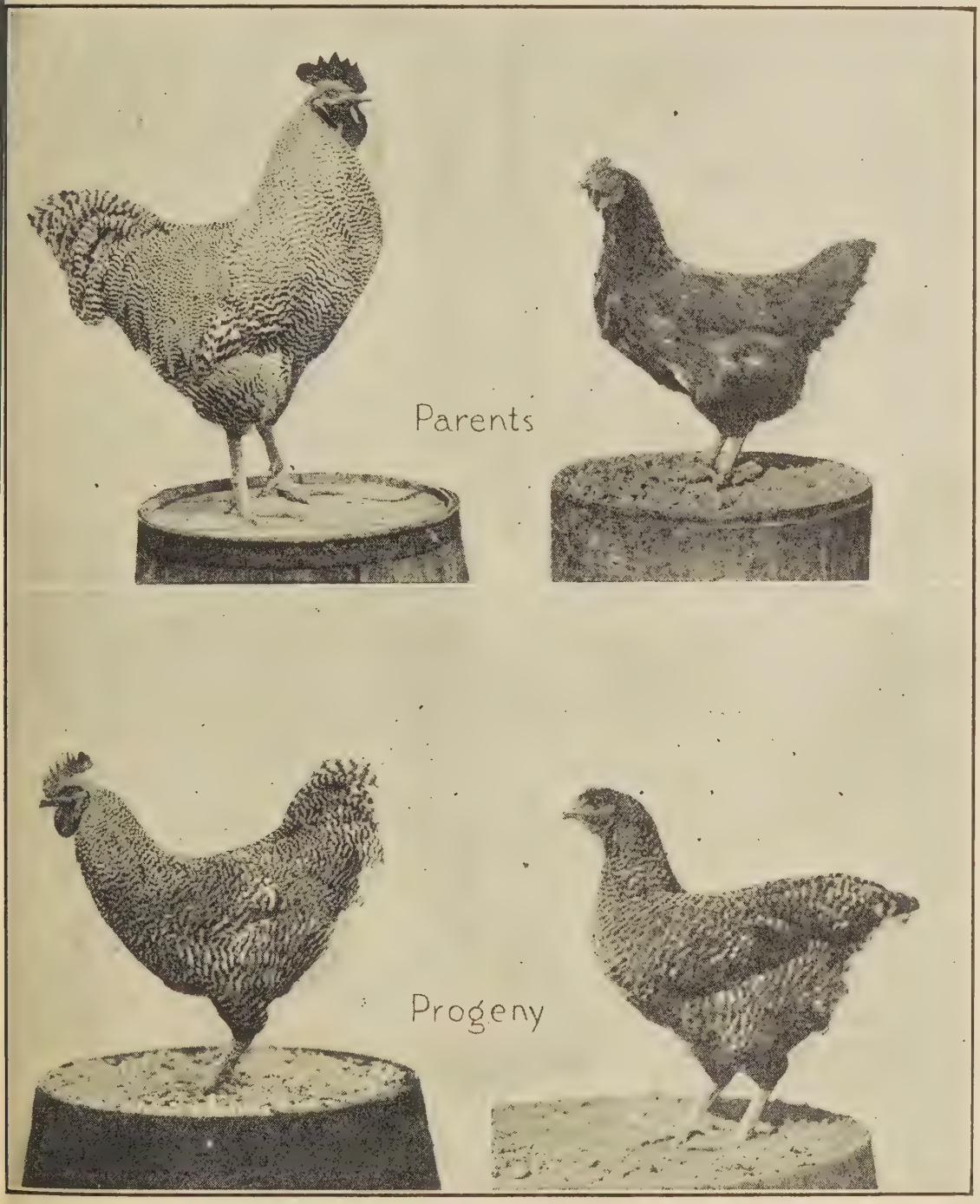

FIG. 17. When a Barred Plymouth Rock male is mated to a nonbarred colored female, such as Rhode Island Red, the daughters as well as the sons are barred. The dominant sex-linked gene, B, for barring is transmitted from the sire to the daughters and to the sons, as shown in Fig. 19. (U. S. D. A.)

for sex-linked genes, whereas in the *XY* type the female is homozygous for sex chromosomes and consequently for sex-linked genes.

The results of a mating between a Rhode Island Red male and a

Barred Plymouth Rock female are illustrated in Fig. 16. The male progeny are barred and the female progeny are black or largely so. Some of the female progeny may have red on the neck and breast feathers, but black is the predominant plumage color.

The results of a mating between a Barred Plymouth Rock male and a Rhode Island Red female are illustrated in Fig. 17. All the progeny, both male and female, are barred.

It is observed that different results are produced in these two matings, depending upon whether the female used was barred or not. The results secured in the reciprocal matings between Rhode Island Reds and Barred Plymouth Rocks demonstrate that the gene that produces barring is sex-linked, inasmuch as the Barred Plymouth Rock female transmits barring to her sons but not to her daughters. A true test of the sex-linkage of the gene for barring is a mating of a Rhode Island Red male and the black females produced from a cross between a Rhode Island Red male and Barred Plymouth Rock females. The progeny of the Rhode Island Red male mated to the black females are nonbarred, showing that the black females did not possess the gene for barring. However, since the Rhode Island Red male when mated to Barred Plymouth Rock females produces barred sons and black daughters, it is obvious that the gene for barring is sex-linked and is transmitted from the barred female parent to her sons only.

Barring Dominant to Nonbarring. The results of the mating between the Barred Plymouth Rock male and Rhode Island Red female demonstrate that the gene for barring is dominant to the gene for nonbarring as in the Rhode Island Red. The term "dominant" simply means that one character dominates or suppresses the other. Although in the *WZ* type of sex inheritance *W* represents the absence of one of the pair of sex chromosomes, the customary way of indicating the absence of a sex chromosome is by the use of a dash, so that the female sex chromosome condition is expressed as *Z*—, whereas the male sex chromosome condition is *ZZ*.

If the symbol *B* be used to denote the sex-linked gene that produces barring, then the genetic constitution of the Barred Plymouth Rock female becomes *ZB*—, and the genetic constitution of the Barred Plymouth Rock male becomes *ZB ZB*, as far as the inheritance of barring alone is concerned. Since barring is dominant to nonbarring, as in the Rhode Island Red, the symbol *b* represents the gene for nonbarring. The genetic constitution of the Rhode Island Red female, therefore, is represented by *Zb*— and that of the Rhode Island Red male by *Zb Zb*.

The results, concerning the inheritance of barring, of the mating between a Rhode Island Red male ($17+Zb$ and $17+Zb$) and a Barred Plymouth Rock female (17— and $17+ZB$) are illustrated in Fig. 18. The Rhode Island Red male produces but one kind of gamete, $17+Zb$, whereas the Barred Plymouth Rock female produces two kinds of gametes, $17+ZB$ and 17—, the 17 autosomes being included merely for the purpose of representing each gamete with its full complement of chromosomes. The scheme in Fig. 18 illustrates a point that should always be kept in mind in similar matings, namely, that either male gamete may fertilize either female gamete.

The mating of the $17+Zb$ male gametes with each of the two female gametes produces the two kinds of zygotes ($17+ZB$ and $17+Zb$) and (17— and $17+Zb$), respectively. The zygotes ($17+ZB$ and $17+Zb$) are in the first place males, because 2 sex chromosomes are present in each zygote, and in the second place barred because the gene for barring (B) is present. The zygotes (17— and $17+Zb$) are in the first place females because only 1 sex chromosome is present in each zygote, and in the second place nonbarred because the gene for barring (B) is absent. The scheme in Fig. 18 shows clearly how the Barred Plymouth Rock female transmits barring to her sons only.

The results of the mating between a Barred Plymouth Rock male ($17+ZB$ and $17+ZB$) and a Rhode Island Red female (17— and $17+Zb$) are illustrated in Fig. 19. The Barred Plymouth Rock male produces but one kind of gamete, $17+ZB$, whereas the Rhode Island Red female produces two kinds of gametes, $17+Zb$ and 17—. The mating of the $17+ZB$ male gametes with each of the two female gametes produces two kinds of zygotes ($17+ZB$ and $17+Zb$) and (17— and $17+ZB$). The zygotes containing 2 sex chromosomes are males, whereas those containing 1 sex chromosome are females, both males and females, however, are barred because the gene for barring (B) is present in each zygote. The scheme in Fig. 19 shows clearly how the Barred Plymouth Rock male transmits barring to his daughters as well as his sons.

Distinguishing the Sexes at Hatching Time. An interesting feature about the inheritance of several sex-linked characters is that the sexes of the chicks can be distinguished at hatching time, thus allowing for the separation of males and females for any particular purpose.

In the case of the mating between a Rhode Island Red male and a Barred Plymouth Rock female, the male chicks at hatching time resemble purebred Barred Plymouth Rock male chicks very closely. There is the characteristic white or light spot on the back of the head,

the under part of the body is grayish, but all the rest of the down is black in color, and the beak and shanks and toes are yellow. The female chicks from the cross are quite different from the males inasmuch as the down color is all black, including the top of the head, and the beak, shanks, and toes are black or very dark in color. The chicks

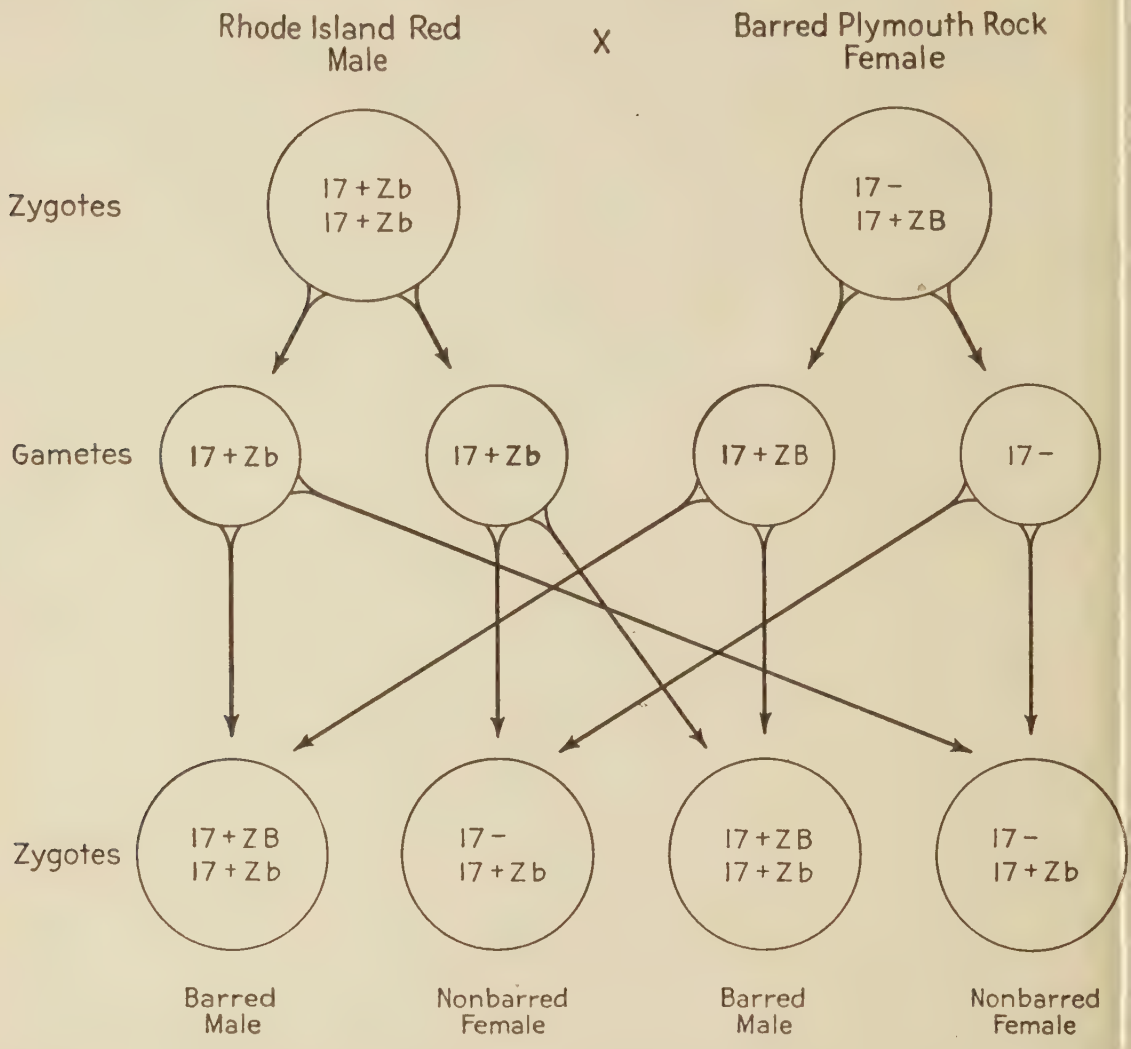

FIG. 18. Showing the manner in which the gene for barring in a Barred Plymouth Rock female is transmitted to her sons only. The gene for barring is indicated by B and the gene for nonbarring by b, each being contained in the sex chromosome, indicated by Z.

can be separated according to sex with a high degree of accuracy. The male chicks develop into barred birds, whereas the female chicks develop into black ones, some perhaps having some red on the neck or breast or both.

Other crosses can be made involving the inheritance of sex-linked characters which make it possible to distinguish the sex of chicks at hatching time. Such cases as well as other sex-linked crosses that do not permit the separation of the chicks according to sex at hatching time are discussed in later sections of the book.

MENDELIAN INHERITANCE

The inheritance of many of the characters possessed by the domestic fowl is a phenomenon of such universal occurrence that it is accepted by most poultrymen as a matter of course, something so evident that it requires no explanation. The possession of feathers is a character

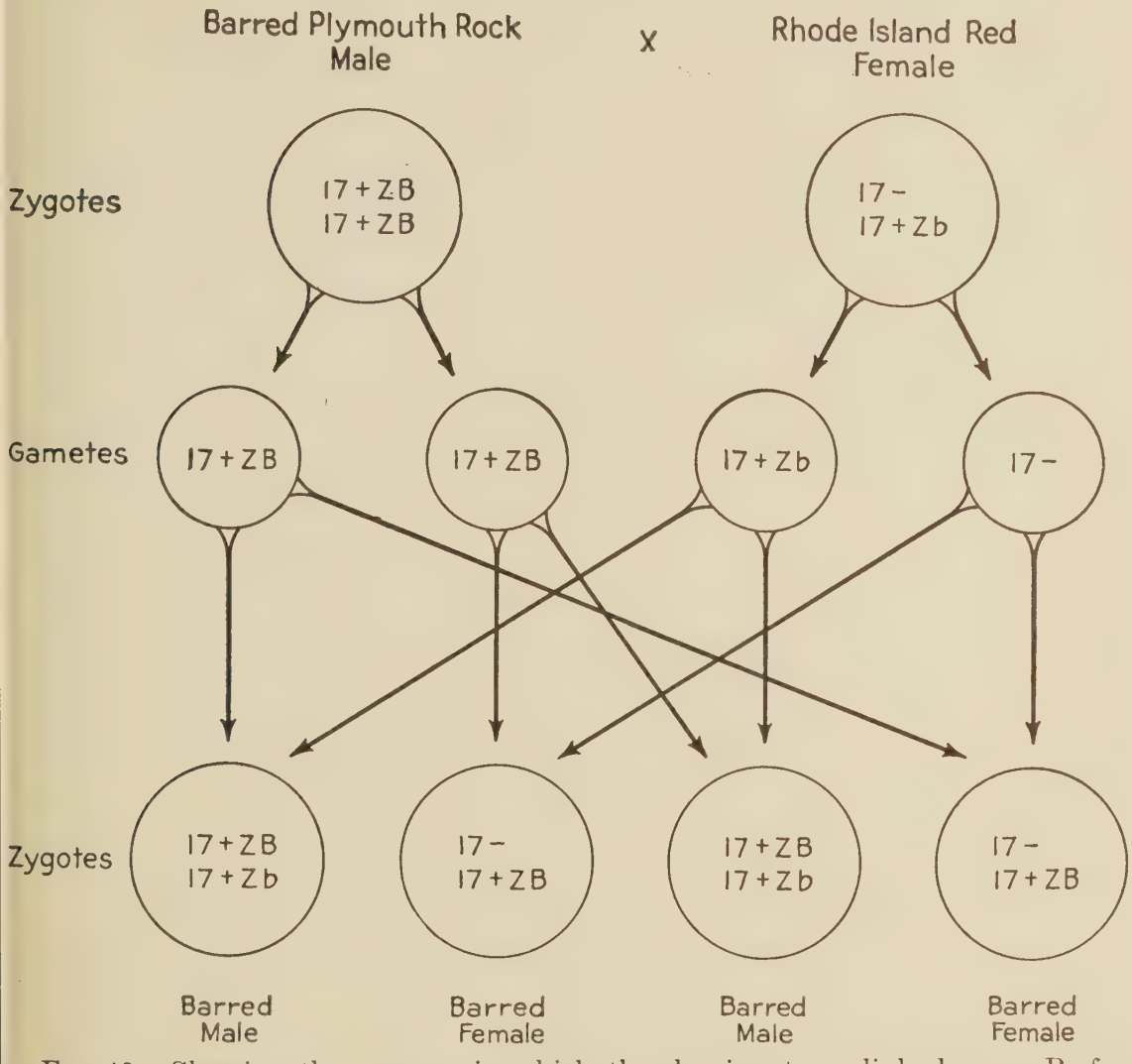

FIG. 19. Showing the manner in which the dominant sex-linked gene, B, for barring is transmitted to the daughters as well as the sons in a mating of Barred Plymouth Rock male × Rhode Island Red female.

confined exclusively to birds, but the fact that some birds have laced feathers while other birds have penciled feathers, and the fact that some birds lay well whereas others do not, are matters that do require explanation if one is to gain a clear understanding of the manner in which the different characters which birds possess are reproduced from one generation to the next. From the standpoint of inheritance, the term character means any one of the many details of form, substance, structure, or function which make up a fowl.

Inheritance is transmission from parent to offspring. The characters are not transmitted bodily, however; for instance, there are no feathers in the egg or on the chick when hatched but the chick possesses the ability to grow feathers. It is the ability, power, or potentiality to develop such characters as white or yellow skin color, barred or spangled feathers, crests, feathered shanks, brown or white color of egg shell, that is inherited. It is the ability to produce an abundant amount of flesh of excellent quality or the ability to lay well that is inherited.

Although it is true that the characters which a fowl possesses are not transmitted bodily, it seems justifiable to speak of the inheritance of characters, as for instance, the inheritance of white and black, of barring, and of egg production. Such a method of discussing the subject of inheritance simplifies the problem of presenting the matter to the layman.

The Significance of Variation. Reference has already been made to numerous characters possessed by domestic fowls, but the fact should be emphasized here that each and every individual fowl possesses a large number of characters. A Barred Plymouth Rock possesses a single comb; barred feathers; red earlobes; yellow skin, beak, and shanks; nonfeathered shanks; four toes, as well as many other characters. A Light Brahma possesses a pea comb, a columbian-colored plumage pattern, and feathered shanks, and has a different build from that of the Barred Plymouth Rock. A White Plymouth Rock, however, has the same build as the Barred variety but differs from it in having white plumage. Moreover, not all White Plymouth Rocks are exactly alike. There is always some difference, however minute, that distinguishes two individuals that are otherwise much alike, and this is as true among men as among domestic fowls.

Since it is true that there are no duplicates among domestic fowls, it is obvious that the old saying "like begets like" cannot be wholly true, for the simple reason that there is no exact likeness between parent and offspring or among brothers and sisters. It is true, of course, that all Leghorns do resemble each other to a marked degree when compared with all Rhode Island Reds, but it is also true that a particular Leghorn may resemble a particular Rhode Island Red much more closely regarding ability to transmit egg production than either of these two birds is resembled by all other members of its breed.

The fact that there is great variation among fowls is of particular significance in inheritance. Without variation, progress in breeding work would be impossible. Without variation, the selection of superior individuals would be impossible. Without selection, improvement is

impossible. Variation makes selection possible, and selection makes improvement possible.

The fact that there is great variation among fowls has made possible the development of the science of breeding upon a very definite basis. Although it is true that there are no two Barred Plymouth Rocks that are exactly alike, it is also true that as long as Barred Plymouth Rocks are mated among themselves nothing but barred birds are produced, except white "sports" very occasionally. Barring is regarded as a stable character that is transmitted regularly from generation to generation, although the quality of barring in any two individuals always differs somewhat.

The character black plumage in Black Langshans, Jersey Black Giants, Black Rose-Comb Bantams, and other black varieties is regarded as a stable character transmitted regularly, except for occasional white "sports" which appear from time to time, when birds of the same variety are mated among themselves.

White Rose-Comb Bantams and other white varieties breed true when bred among themselves so that the character white plumage is regarded as stable.

But when fowls possessing unlike characters are mated together some very interesting and sometimes very surprising results are secured. The manner in which black and white are inherited in a cross between Black Rose-Comb and White Rose-Comb Bantams serves to illustrate the kind of results secured in the inheritance of most pairs of characters. In this case black is one character and white the other; in presenting the results secured in the form of tables it is a matter of convenience to denote the different generation of families by symbols. The parental generation, meaning the parents used in the first cross, is designated by the symbol P_1. The family or progeny secured from the original cross or mating is known as the first filial generation and is designated by the symbol F_1. When members of the first filial generation are mated among themselves they produce the second filial generation, which is designated by the symbol F_2. Briefly then, P_1 produces F_1, and F_1 produces F_2.

The manner in which the characters black and white are inherited in a cross between Black Rose-Comb and White Rose-Comb Bantams will serve to illustrate the mechanism involved in the inheritance of most pairs of characters. The first, and, so far as can be determined, the only reference to such a cross having been made is reported by Bateson and Punnett (1908). They mated Black Rose-Comb Bantams to White Rose-Comb Bantams and secured black progeny only. They mated 3 of the F_1 black females to 1 of the F_1 black males and secured

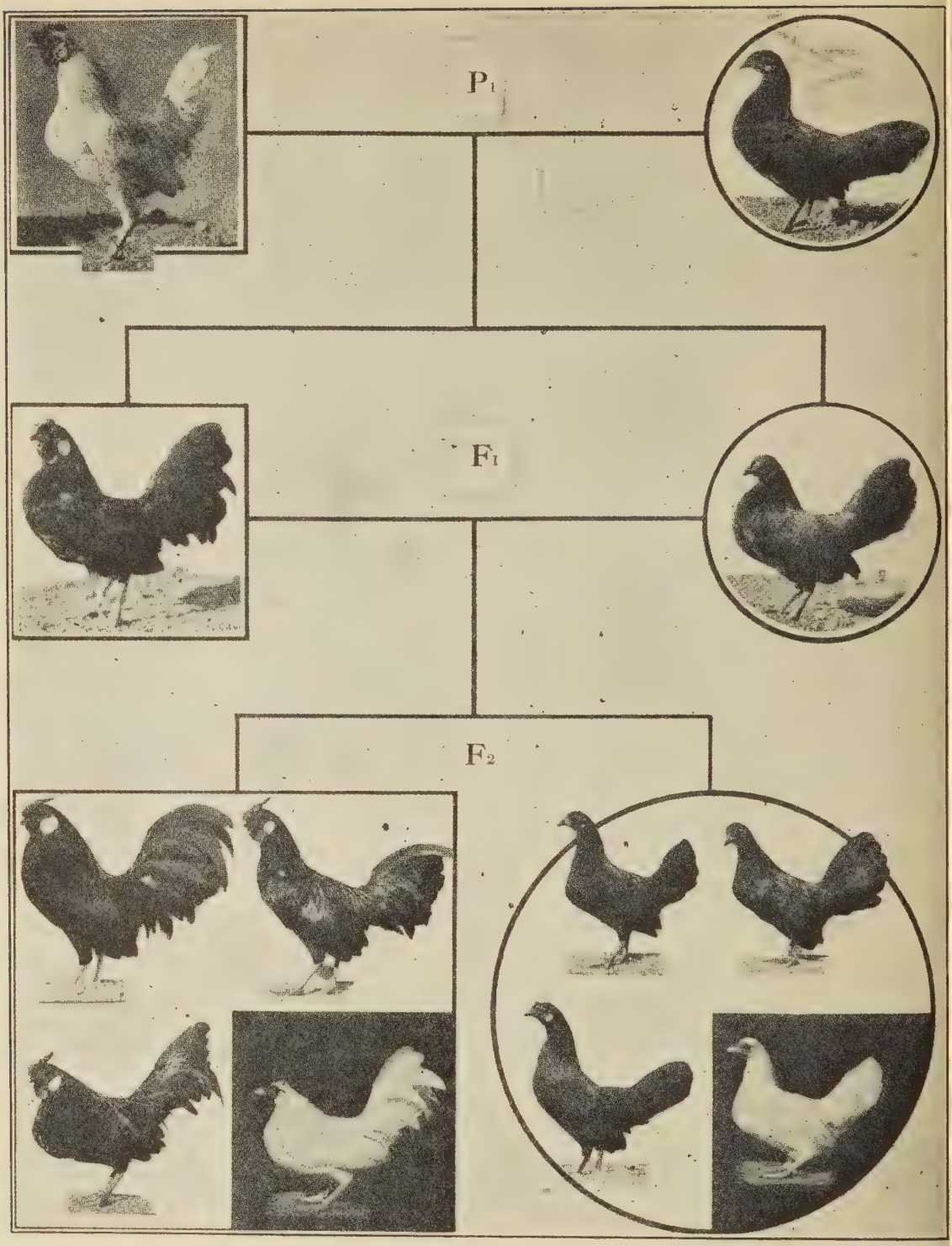

FIG. 20. A White Rose-Comb Bantam male mated to a Black Rose-Comb Bantam female (the P_1 generation) produces offspring (the F_1 generation), all of which are black. In this mating the gene for black plumage is dominant and the gene for white plumage is recessive so that all the F_1 birds are black although each has received a dominant gene for black from the female parent, and a recessive gene for white from the male parent, the genes for black and for white being contained in the autosomes. When an F_1 male is mated to an F_1 female an F_2 generation is produced consisting of 3 blacks to 1 white, in both sexes. In each sex 1 black out of every 3 is pure for black whereas the other two blacks each carry the gene for white as well as black. The F_2 white birds are pure for white, so that when they are bred among themselves they produce nothing but white offspring. The appearance of white birds in the F_2 generation illustrates the principle of the segregation of the genes. In the F_1 generation the genes for black and for white were combined whereas in the F_2 generation they segregated to give a proportion of 3 to 1. (Photo by Jull and Quinn in Jour. Hered.)

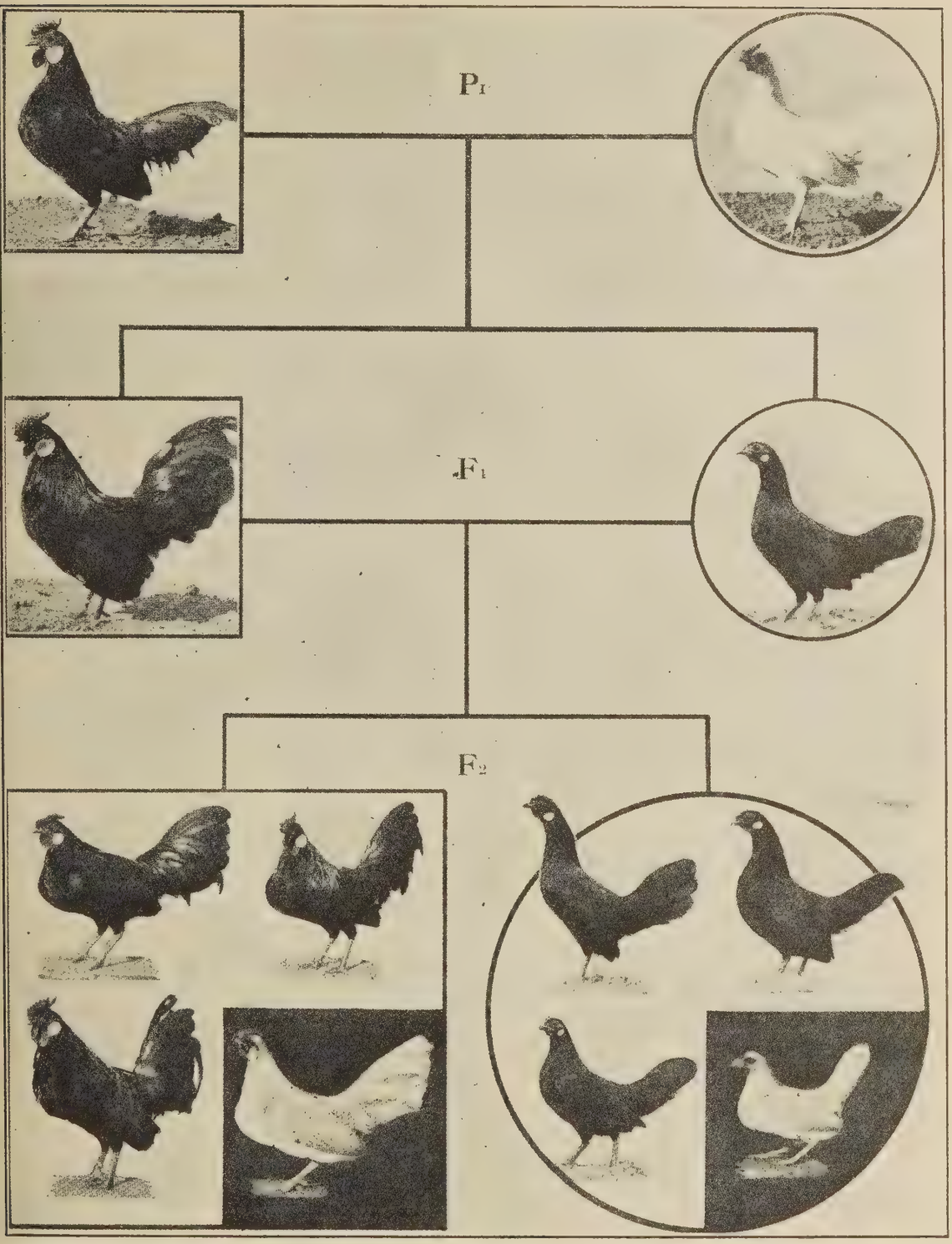

FIG. 21. A Black Rose-Comb Bantam male mated to a White Rose-Comb Bantam female (the P_1 generation) produces offspring (the F_1 generation), all of which are black, as in the reciprocal cross illustrated in Fig. 20. Similar results are secured in the F_2 generation, 3 blacks to 1 white, due to the well established Mendelian principle of the segregation of the genes. The results secured in this cross and in the cross illustrated in Fig. 20 demonstrate that the genes for black and for white are contained in the autosomes and not in the sex chromosomes. See Figures 22 and 23 which show clearly how the proportion of 3 blacks to 1 white is secured in the F_2 generation of the crosses illustrated. (Photo by Jull and Quinn in Jour. Hered.)

70 black and 24 white progeny. This approximates very closely a ratio of 3 blacks to 1 white.

The results of crosses between White Rose-Comb and Black Rose-Comb Bantams secured at the U. S. Animal Husbandry Experiment Farm, Beltsville, Maryland, are given, together with photographs of birds used in the various matings. In the spring of 1927 one pen of 5 White Rose-Comb Bantam males mated to 17 Black Rose-Comb Bantam females produced 107 progeny, all of which were black. During the same breeding season another pen of 2 Black Rose-Comb Bantam males mated to 5 White Rose-Comb Bantam females produced 39 progeny, all of which were black. It is observed that both crosses produced black progeny.

During the breeding season of 1928 two matings were made. The first mating consisted of black brothers and black sisters from the first mating of 1927, White Rose-Comb Bantam males and Black Rose-Comb Bantam females. Observations were made on the color of the chicks that died in the shell at hatching time as well as those which hatched and matured. Among the chicks that died there were 81 black and 24 white chicks. Among the chicks which hatched and matured there were 189 black and 65 white chicks. Among the total progeny, therefore, there were 270 black and 89 white chicks, a ratio approximating closely 3 to 1.

The second mating made in 1928 consisted of the black brothers and black sisters from the second mating of 1927, Black Rose-Comb Bantam males and White Rose-Comb Bantam females. Among the chicks that died in the shell at hatching time there were 21 black and 9 white chicks. Among the chicks that hatched and matured there were 29 black and 9 white chicks. The total progeny, therefore, gave 50 black and 18 white chicks, again a fairly close approximation of a 3-to-1 ratio.

Both matings made in 1928 gave 320 black and 107 white chicks, almost exactly a 3-to-1 ratio. The results are shown in Table 6.

The results secured in this simple experiment involving one pair of characters demonstrate two important features. The first important feature is the demonstration of the fact that in this particular cross the first filial generation are all black in spite of the fact that one of the parents is white. The second important feature is the fact that in the second filial generation the two characters black and white appear in the proportion of approximately 3 blacks to 1 white.

These two features constitute the basic principles of Mendelian inheritance, which simply means the theory of inheritance first propounded by Gregor Mendel, a monk, and later abbot, in the Franciscan

TABLE 6. F_2 RESULTS SECURED IN RECIPROCAL CROSSES BETWEEN BLACK ROSE-COMB AND WHITE ROSE-COMB BANTAMS

(Jull and Quinn, 1929)

Kind of Mating		No. Black Progeny	No. White Progeny	Proportion (Black:1 White)
Sons mated to daughters of 1927 mating of White males and Black females.	Died in shell	81	24	3.375
	Hatched	189	65	2.908
	Total	270	89	3.034
Sons mated to daughters of 1927 mating of Black males and White females.	Died in shell	21	9	2.333
	Hatched	29	9	3.222
	Total	50	18	2.778
Totals from both matings		320	107	2.991

Monastery at Brno, Austria. Mendel carried on breeding experiments with peas and other plants, and the results he secured became the foundation of most of the modern work on inheritance of characters in plants and animals. Mendel's results were published in 1866 but attracted little attention at the time and remained practically unknown for 35 years until brought to light in 1900 by three investigators. Bateson (1902), working with the domestic fowl, was the first to demonstrate that the Mendelian principles of inheritance apply to animals.

During recent years, the results secured from many matings demonstrate that numerous characters of the domestic fowl are inherited in typical Mendelian manner. Most of these characters are simple ones, involving, for the most part, color and structural characters. Determining the mode of inheritance of more complicated characters, such as hatchability and egg production, still awaits solution, although much progress has been made.

The Principle of Dominance. It has already been noted that in the cross between Black Rose-Comb and White Rose-Comb Bantams all the F_1 progeny are black. The gene for white was transmitted in exactly the same manner as the gene for black, but none of the F_1 birds shows any white in its plumage. Each zygote giving rise to an F_1 bird contains a gene for black and a gene for white, but a black bird is the result. Black is dominant to white in this particular

cross, and the principle of dominance was the first basic principle of inheritance that Mendel discovered. Bateson and Punnett (1906) observed that the white of the White Rose-Comb Bantam is recessive to color.

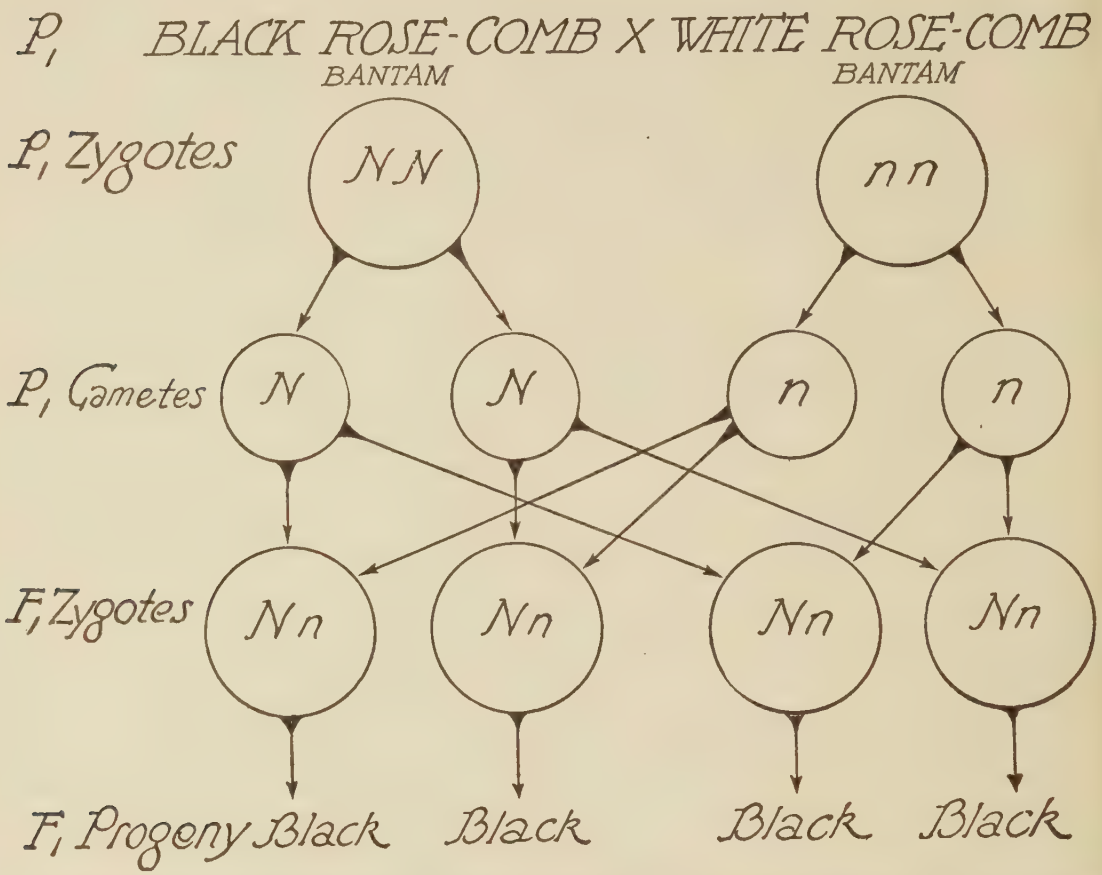

FIG. 22. The parental (P_1) zygotes give rise to the parental (P_1) gametes and these gametes unite in pairs to form the F_1 zygotes, which develop into the F_1 progeny or F_1 generation or F_1 hybrids. The F_1 or first hybrid generation birds are black, since *N*, for nigrant or black plumage, is dominant to *n*, for white plumage. The sex chromosomes are not represented in the zygotes or gametes because the genes *N* and *n* are each contained in one of the 17 autosomes and it makes no difference which way the cross between black and white in Rose-Comb Bantams is made, the results secured are the same, as has been shown in Figs. 20 and 21.

Since in this cross black is dominant to white, the character black is represented by the capital letter *N*, meaning nigrant or black, and the recessive character white is represented by the small letter *n*, meaning the absence of nigrant or black. (See Fig. 22.) Furthermore, since genes are responsible for the development of the hereditary characters black and white, the genes are represented by the letters *N* and *n*, respectively. The zygote of the purebred Black Rose-Comb Bantam contains the genes *NN* and the zygote the purebred White Rose-Comb Bantam contains the genes *nn*.

It should be pointed out at this time that the symbols *N* for black

and *n* for white are used here purely as a matter of convenience although the proper symbols which correctly express the difference between black and white plumage in Rose-Comb Bantams are given in the next chapter, where the difference is shown to be rather complex. The symbols *N* and *n* are used at this time for the sake of simplicity in illustrating the principle of dominance of one character over another

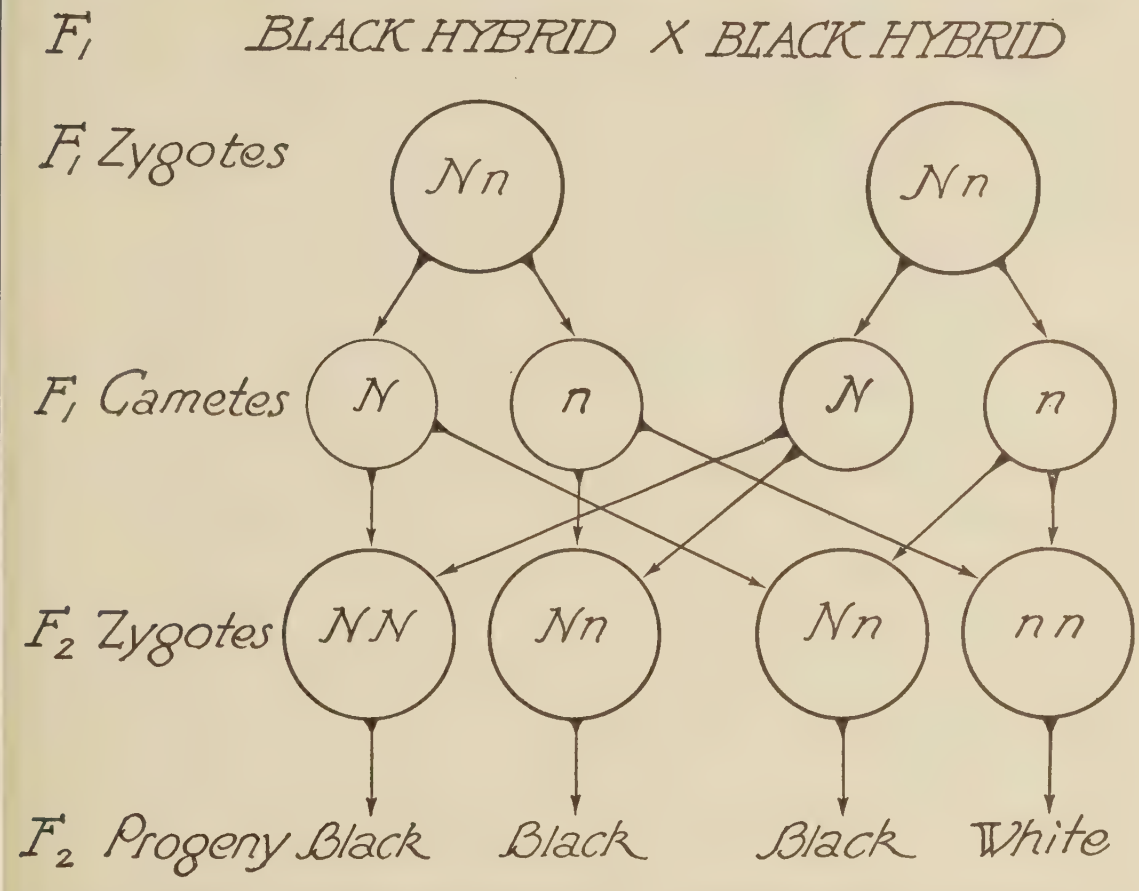

FIG. 23. The F_1 zygotes give rise to the F_1 gametes and these gametes unite in pairs to form the F_2 zygotes, which develop into the F_2 progeny. The color of the progeny is in the proportion of 3 blacks to 1 white. Among the blacks, 1 is homozygous and 2 are heterozygous for black. The homozygous black and the homozygous white are the same kind of birds as the original parents; see P_1 zygotes in Fig. 22.

and the principle of the segregation of characters. The symbol *B* is not used for black because *B* has been used in the previous chapter for barring.

Homozygous and Heterozygous. The constitution of the zygote of the purebred black parent (*NN*) is spoken of as being "homozygous," which simply means that in this case two similar genes are contained in the zygote or mature bird. The constitution of the zygote of the white parent (*nn*) is also in the homozygous condition. On the other hand, the constitution of the zygote of each of the first filial generation birds is *Nn*, and this condition is spoken of as being

"heterozygous," which simply means that in this case two different genes are contained in the zygote or mature bird.

Different Kinds of Gametes Formed by F_1 (Heterozygous) Birds. Although all the birds of the first filial generation resemble the black parents, they do not give the same results in breeding. An F_1 male (*Nn*) and female (*Nn*) each produces two kinds of gametes *N* and *n*, as shown below and in Fig. 23. In the male, therefore, there is an equal number of gametes containing the *N* and the *n* genes, respectively, and in the female there is an equal number of gametes containing the *N* and the *n* genes, respectively. When the male and the female gametes unite to form the new zygote, four possible combinations occur in approximately equal numbers, as follows:

N male gamete × *N* female gamete = *NN* zygote—black.
N male gamete × *n* female gamete = *Nn* zygote—black.
n male gamete × *N* female gamete = *Nn* zygote—black.
n male gamete × *n* female gamete = *nn* zygote—white.

A very convenient way of showing the kind of zygote formed by the gametes is by use of the checkerboard principle, as shown in Fig. 24. The male gametes are placed on the left side of the squares of the checkerboard and the female gametes are placed on the top of the squares of the checkerboard. As each gamete of one sex is mated to each gamete of the opposite sex the product is placed in the appropriate square.

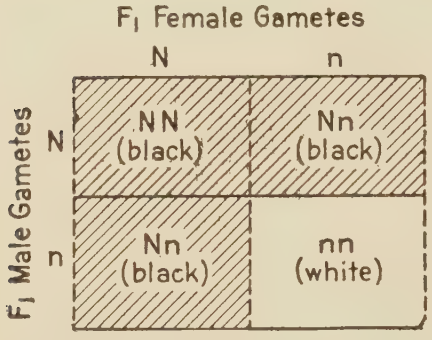

FIG. 24. Showing the F_2 results produced by a mating of an F_1 male × F_1 female, each of the F_1 birds being black because in this cross black is dominant to white. The F_2 generation consists of the proportion of 3 blacks to 1 white.

Different Kinds of F_2 Birds Produced. The colors of the F_2 progeny arising from the four zygotes formed are shown in brackets. There are three blacks to one white. One of the blacks (*NN*) is homozygous for the dominant character; the other two blacks (*Nn*) are heterozygous for both characters; and the white (*nn*) is homozygous for the recessive character.

The first black (*NN*) always breeds true; that is, when these birds are bred among themselves they produce nothing but blacks, simply because both males and females can produce only gametes containing the *N* gene and when these unite *NN* zygotes are formed. The two blacks in the equations above each with the *Nn* zygote are heterozygous and produce the same results as their parents, the birds of the

first filial generation. The white bird (*nn*) is homozygous for the recessive character, and when such birds are bred among themselves they produce nothing but whites simply because each gamete formed contains the *n* gene, and when these gametes unite nothing but *nn* zygotes are formed.

The fact that there is dominance of one character over another has been demonstrated many times in poultry-breeding work. There are cases, however, where the dominance is not complete but only partial. These and other related problems are discussed later.

The Principle of Segregation. In the cross between two contrasting characters, black and white, it has already been observed that in the first filial generation one character dominated the other but in the second filial generation there was a segregation of the characters so that the two contrasting color characters appeared in the proportion of 3 blacks to 1 white. Two contrasted characters brought together in F_1 become separated from each other in F_2.

Furthermore, it has also been observed that in the F_2 generation there are blacks that breed true, producing nothing but blacks, and the whites breed true, producing nothing but whites. There are also blacks that do not breed true, for when they are mated among themselves they produce progeny in the ratio of 3 blacks to 1 white, if sufficient numbers are raised. Therefore, although the F_2 generation is comprised of 3 blacks to 1 white, the blacks differ in respect to the results they produce when they are bred. Among every 3 blacks 1 is homozygous whereas the other 2 are heterozygous for color, so that the F_2 ratio is really 1:2:1—1 homozygous black, 2 heterozygous for each black and white, and 1 homozygous for white—that is, 1 *NN*:2 *Nn*:1 *nn*.

The demonstration of the segregation of character in the F_2 generation and the concurrent demonstration of the segregation of the genes as separate units is the first of two major contributions Mendel made to the science of breeding. The establishment of the principle of segregation gave birth to a new conception concerning the manner in which characters are inherited from generation to generation and led to remarkable discoveries concerning the mechanism of inheritance.

The Principle of Independent Assortment. The second of two major contributions Mendel gave to the science of breeding is the demonstration of the principle of the independent assortment of the genes. This principle is clearly illustrated in the case of the inheritance of two pairs of characters.

The inheritance of two pairs of characters is precisely the same in principle as the inheritance of one pair. Since two pairs of char-

acters are involved, the F_1 hybrids are able to produce four kinds of gametes instead of only two, as in the case of the inheritance of one pair of characters. Since four kinds of gametes are produced by each sex, the possibilities for the segregation and recombination of the genes is four times as great as in the case when only two kinds of gametes are formed, as shown in Fig. 25.

The rose comb is the standard type in Rose-Comb Bantams but occasionally a bird with a single comb appears. As shown in Chapter V, rose comb is dominant to single comb. Therefore, if Black Rose-Comb Bantams are crossed with white single-comb bantams two pairs of characters are involved in the cross: black plumage and white plumage as one pair, and rose comb and single comb as the other pair.

By using appropriate symbols to designate the genes carried in the chromosomes the mode of inheritance of the two pairs of characters is readily demonstrated. Capital letters are used for the dominant characters and small letters for the recessive characters. *R* represents the rose-comb character and the gene that produces it, *r* the single-comb character and the gene that produces it, *N* the black character and the gene that produces it, and *n* represents the white character and the gene that produces it. Since the genes are borne in pairs, the zygote of the Black Rose-Comb Bantam contains the genes *RRNN* and the zygote of the white single-comb bantam contains the genes *rrnn*, the Black Rose-Comb Bantam being homozygous for both rose comb and black and the white single-comb bantam being homozygous for both single comb and white.

The Black Rose-Comb parent produces *RN* gametes and the white single-comb parent produces *rn* gametes; these unite to form the F_1 zygote *RrNn*. Such zygotes are heterozygous for both pairs of characters, but the presence of *R* and *N* makes the F_1 birds rose-comb black. The F_1 male zygote produces four kinds of gametes (sperm): *RN, Rn, rN, rn;* and, likewise, the F_1 female zygote produces the same four kinds of gametes (eggs): *RN, Rn, rN, rn.* Each male gamete may mate with each female gamete, so that there are 16 possible combinations. The checkerboard plan of illustrating the kind of zygote formed by the mating of any two gametes is very effective, as shown in Fig. 25.

The type of comb and the color of the bird arising from each of the 16 zygotes formed are given in brackets in each square in Fig. 25. Of the 16 zygotes formed it is observed that they give rise to 9 rose-comb blacks, 3 rose-comb whites, 3 single-comb blacks, and 1 single-comb white, a 9:3:3:1 ratio. If comb alone is considered, however,

it is apparent that there are 12 rose combs and 4 single combs, a 3:1 ratio. Also, if color alone is considered it is seen that there are 12 blacks and 4 whites, a 3:1 ratio.

Of the 16 F_2 birds, 12 are black, of which 9 are rose combs and 3 are single combs, a 3:1 ratio. Of the 16 F_2 birds, 4 are white, of which 3 are rose combs and 1 is a single comb, a 3:1 ratio. That is, for either pair of characters considered separately, a 3:1 ratio results.

New Types Produced. It is interesting to observe that the mating of Black Rose-Comb Bantams and white single-comb ban-

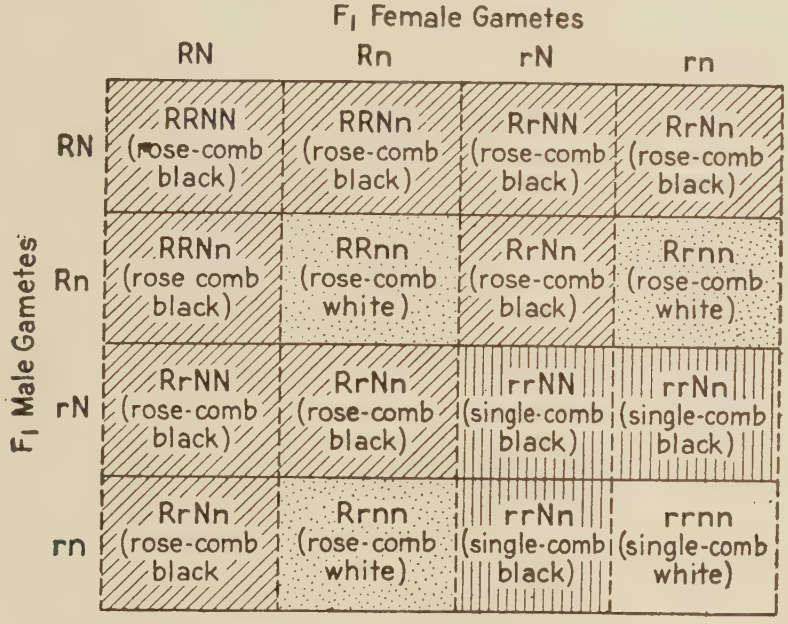

FIG. 25. Showing the F_2 results produced by a mating of an F_1 male × F_1 female, each of the F_1 birds being rose-comb black because rose comb is dominant to single comb and black is dominant to white. The F_2 generation consists of a ratio of 9:3:3:1, due to the Mendelian principle of the independent assortment of the genes.

tams has produced in the F_2 generation four kinds of birds: rose-comb blacks, rose-comb whites, single-comb blacks, and single-comb whites. The rose-comb blacks and the single-comb whites are the same kind as the parents, but the rose-comb whites and the single-comb blacks are new types. How did these new types arise?

The parental zygotes are *RRNN* and *rrnn*. The F_1 zygotes are all of one kind, *RrNn*. F_2 zygotes, as observed in the checkerboard, are as follows:

1 *RRNN*—homozygous rose comb and homozygous black 2 *RRNn*—homozygous rose comb and heterozygous black 2 *RrNN*—heterozygous rose comb and homozygous black 4 *RrNn*—heterozygous rose comb and heterozygous black	}	9
1 *RRnn*—homozygous rose comb and homozygous white 2 *Rrnn*—heterozygous rose comb and homozygous white	}	3

1 *rrNN*	—homozygous single comb and homozygous black	3
2 *rrNn*	—homozygous single comb and heterozygous black	
1 *rrnn*	—homozygous single comb and homozygous white	1
16		16

The 16 birds include 9 different kinds of birds according to the combination of genes they contain, and it should be observed that the first one, *RRNN,* and the last one, *rrnn,* are the same as the parents used in the original cross. The 3 rose-comb whites and the 3 single-comb blacks are new types which differ from both parents. The only way in which these new types shown could be produced is through the independent assortment of the genes for plumage color and for type of comb. The gene for rose comb is just as apt to be associated with the gene for black as it is with the gene for white, and the same is true of the gene for single comb.

These 16 birds are made up of 4 groups of birds according to type of comb and plumage color, as indicated by the brackets on the right side of the list of the 16 zygotes. The first group includes 9 rose-comb blacks; the second group, 3 rose-comb whites; the third group, 3 single-comb blacks; the fourth group, 1 single-comb white.

The reason that there is a 9:3:3:1 ratio in the F_2 generation involving the inheritance of two pairs of characters is the dominance of rose over single comb and the dominance of black over white. The 9:3:3:1 ratio is precisely what should be expected when each member of two pairs of characters is inherited independently of the others. A 9:3:3:1 ratio in the F_2 generation would result from an original cross of White Rose-Comb Bantams, (*RRnn*), and black single-comb bantams, (*rrNN*), instead of the parents that were used in the former cross, Black Rose-Comb Bantams and white single-comb bantams. It is apparent, therefore, that the same results are secured in the F_2 generation regardless of the way in which the characters entered the cross. In other words, the particular combination in which the characters are brought into a cross makes no difference at all in the manner in which they are assorted and recombined in the F_2 generation.

In one cross both dominant characters were brought in by one parent, *RRNN,* and both recessive characters by the other parent. *rrnn*; whereas in the other cross one dominant and one recessive character were brought in by each parent, *RRnn* and *rrNN*. Both crosses produce the same results in the F_2 generation, showing clearly that the genes responsible for the two pairs of characters assort themselves

independently of each other and recombine in definite proportions. The principle of the independent assortment of the genes is fundamentally important to a proper understanding of the general problem of inheritance.

The F_2 Ratio in Relation to Pairs of Genes in Original Cross. In crosses in which more than two pairs of independent characters are involved, the segregation and independent assortment of the genes occur in precisely the same way as in the inheritance of one pair or two pairs of independent characters. It will be recalled that in the case of one pair of characters two kinds of F_1 gametes are formed, and in the case of two pairs of characters four kinds of F_1 gametes are formed. The number of different kinds of gametes formed by the F_1 birds is doubled with each increase in the number of different genes involved.

In the inheritance of three pairs of characters eight kinds of F_1 gametes are formed, and in the inheritance of four pairs of characters sixteen kinds of F_1 gametes are formed. Each time the different genes involved are increased by one the number of F_1 gametes formed is increased by two. On the other hand, for each increase in the number of different genes involved, the average number of F_2 individuals required to be produced to secure the appearance of the various combinations of characters resulting from the chance combination of the different kinds of F_1 gametes is increased by four, as shown in Table 7.

It becomes clear, therefore, that, regardless of the number of independent characters involved in the original cross, the mode of inheritance is the same, and the different types produced in the F_2 generation always bear a certain mathematical proportion, depending upon the number of independent pairs of genes involved.

Three Fundamental Principles of Mendelian Inheritance. The discussion in this chapter brings out clearly the three fundamental principles of inheritance established by the work of Mendel. The first is the principle of the dominance of one character over another of a given pair so that when a bird is heterozygous for both characters only the dominant one is visible. The second is the principle of the segregation of the genes, whereby a gene for a dominant character from one parent and a gene for a recessive character from another parent coming together in the F_1 generation segregate in the F_2 generation as demonstrated by the appearance of true-breeding dominant and recessive types in F_2. The third is the principle of the independent assortment of the genes in inheritance, as demonstrated in the appearance in the F_2 generation of new types possessing characters

TABLE 7. SHOWING, FOR EACH INCREASE IN THE NUMBER OF DIFFERENT PAIRS OF GENES, THE NUMBER OF DIFFERENT KINDS OF F_1 GAMETES FORMED, THE F_2 RATIO, AND THE AVERAGE NUMBER OF F_2 INDIVIDUALS NECESSARY TO SECURE THE APPEARANCE OF ALL POSSIBLE COMBINATIONS OF CHARACTERS

Number of Different Pairs of Genes in the Cross	Number of Different Kinds of F_1 Gametes Produced	The F_2 Ratio	Average Number of F_2 Individuals Necessary to Secure the Appearance of All Possible Combinations of Characters
1	2	3:1	4
2	4	9:3:3:1	16
3	8	27:9:9:9:3:3:3:1	64
4	16	81:27:27:27:27:9:9:9:9:9:9:3:3:3:3:1	256
n	2^n	$(3:1)^n$	4^n

in different combinations from those of either of the parents in the original cross.

Such are the fundamental principles of Mendelian inheritance. They have constituted a notable contribution to the science of breeding, for they have enabled man to produce results with increasing rapidity and precision. In view of the great variety of plumage color patterns and structural features among domestic fowls that have been developed out of the original wild types, it is true that "it is hardly too much to say that we are beginning to look upon the whole organic world as a storehouse of potentialities which may be realized in whatsoever permutations and combinations we may desire." (Dendy, 1919.)

A knowledge of the fundamental principles of Mendelian inheritance enables one to predict the results to be secured from many matings. Dendy (1919) further observes: "By appropriate mating of carefully selected individuals we may introduce good features and eliminate bad ones, and so literally build up races of plants or animals to suit our special needs." But that is not all; in fact, it is not the most important service which Mendel's work has done for the science of breeding. Mendel's greatest achievement was, as Darbishire (1913) points out, "The establishment of the principle that the contents of the germ-cells, and not the outward characteristics of the animals and plants dealt with, must be our guide in breeding."

With many poultry breeders the practice has been to select breeding stock based upon its appearance or its pedigree. Mendelism shows that this is not good enough; the progressive poultry breeder must consider the kind of offspring produced to determine the worth of any bird as a breeder. Instead of looking to the ancestry only, one should also consider the offspring; in fact, in many cases the kind of offspring produced is the only reliable criterion in determining the breeding value of any individual. The progeny test is of paramount importance in successful breeding operations.

MENDELISM AS BASIS OF PRESENT-DAY KNOWLEDGE OF INHERITANCE

Since the rediscovery in 1900 of the illuminating results which Mendel secured and which gave rise to the three fundamental principles of inheritance—dominance, the segregation of genes, and the independent assortment of the genes—results have been secured which show that in certain cases there are modifications of the original concepts on which Mendelism is based. These modifications do not detract from the validity of the Mendelian theory of inheritance but merely show that the inheritance of certain characters is more complex than that of the characters with which Mendel dealt.

Lack of Dominance. In certain cases there is a lack of dominance of one character over the other. For instance, when two breeds that differ widely in body weight are crossed, the F_1 birds are usually intermediate in weight, as pointed out in Chapter V. Lack of apparent dominance is due to the fact that several genes are responsible for the size that a given bird attains.

Different Kinds of Genes According to the Effects They Produce. In the cross between Black Rose-Comb Bantams and white single-comb bantams, discussed previously in this chapter, the genes involved each produced a specific effect, but there are instances where two different genes have a complementary effect and give rise to an F_2 ratio of 9:7 instead of 9:3:3:1. The manner in which such a ratio results is given in a subsequent chapter. The genes in question are called **complementary genes.**

There are cases in which genes belonging to different pairs, although inherited independently, affect one another as they express themselves in the characteristics of the individual, so that a given character depends upon the **interaction of two or more genes.** In poultry one of the most notable examples of such a situation is found in comb inheritance. Rose comb breeds true and pea comb breeds true, but when rose-comb and pea-comb fowls are crossed the F_1

generation has walnut combs. As explained in Chapter V, an interaction takes place between the genes for rose comb and the genes for pea comb so that an entirely new type of comb is produced.

A number of cases have been discovered in which two or more genes not only affect the same character but affect it in the same way, such genes being shown as **duplicate genes**. Then again, several genes may interact to produce a given effect, one of the genes determining the presence of a certain character while the other genes affect the degree of the development of the same character or otherwise modify the expression of the principal gene. Such genes are called **modifying genes**. Still other instances have been found where **a single gene affects several characters**, and occasionally a gene is found which produces such an extreme modification in the development of the embryo as to cause its death, such a gene being known as a **lethal gene**. Illustrations of these various types are given in subsequent chapters.

Modern Terminology. During recent years remarkable advances have been made by investigators in their studies on the inheritance of many characters, some of which have been found to be rather complex. In the literature dealing with inheritance problems certain terms have acquired common usage; since in subsequent chapters a number of these terms are used, they are explained at this time as a matter of convenience to the reader.

When a cross is made between one pair of contrasting characters, such as black and white, the cross is called a **monohybrid** cross and the F_2 ratio of 3:1 is called a monohybrid ratio. A cross involving two pairs of contrasting characters, such as black and white and single comb and rose comb, is called a **dihybrid** cross and the F_2 ratio of 9:3:3:1 is called a dihybrid ratio. A **trihybrid** cross involves three pairs of contrasting characters.

Two terms that occur frequently in the literature dealing with inheritance studies in plants and animals are **genotype** and **phenotype**. The difference in the meaning of these terms is made clear by referring to the results secured in the F_2 generation from the original cross between Black Rose-Comb Bantams and white single-comb bantams. It has already been observed that the following results were secured:

$$\left.\begin{array}{l} 1\ RRNN \\ 2\ RRNn \\ 2\ RrNN \\ 4\ RrNn \end{array}\right\} \text{9 rose-comb black}$$

1 *RRnn*
2 *Rrnn* } 3 rose-comb white

1 *rrNN*
2 *rrNn* } 3 single-comb black

1 *rrnn* 1 single-comb white.

There are 9 groups of birds differing in genetic constitution, including: *RRNN, RRNn, RrNN, RrNn, RRnn, Rrnn, rrNN, rrNn,* and *rrnn.* Each of these groups is called a **genotype.**

There are 4 groups of birds differing in type of comb and plumage color, including: 9 rose-comb blacks, 3 rose-comb whites, 3 single-comb blacks, and 1 single-comb white. Each of these groups is called a **phenotype**, meaning that all the birds in each group look alike.

A group of birds belonging to one phenotype may include several genotypes, as for instance, the phenotype of 9 rose-comb blacks comprises the 4 following genotypes: *RRNN, RRNn, RrNN,* and *RrNn.*

Another term that is used frequently in the literature on inheritance is **allelomorph**, which has a very simple meaning. It has been demonstrated in this chapter that for each character there is always a contrasting character, such as black plumage and plumage that is not black. Another pair of contrasting characters noted in this chapter is rose comb and a comb that is not rose. Such pairs of characters are termed **allelomorphic** pairs, each of the two characters being the allelomorph of the other. The same term is applied to the contrasting pairs of genes which give rise to the contrasting pairs of characters. Genes that are allelomorphs are called **alleles** and occupy the same **locus** in homologous chromosomes.

Multiple allelomorphs constitute more than one changed condition in the same locus of homologous chromosomes, each allelomorph producing a visibly different effect.

A condition known as **epistasis** occurs in the White Leghorn. As pointed out in the next chapter, the White Leghorn carries genes for color and for barring, but they have no effect on the appearance of the bird because there is also present a gene which inhibits or prevents color from being expressed. A gene which thus prevents the expression of another nonallelomorphic gene is said to be **epistatic** to it. The gene which is prevented from expressing itself is said to be **hypostatic** to the other gene.

It is important to distinguish clearly between dominance and epistasis and between recessiveness and hypostasis. The terms dominance and recessiveness are applied to the behavior of alternative

characters based upon genes occupying the same locus in a chromosome, such genes being allelomorphs. The gene *I*, which inhibits the development of color in the White Leghorn, is the allelomorph of *i*, which allows color to be expressed, as in many different varieties. *I* and *i* occupy the same locus in a chromosome. But the White Leghorn also carries the gene *B* for barring and genes for color, as explained in the next chapter, but these genes have no effect because the white of the White Leghorn is epistatic to barring and to color. The genes *I* and *B* and the genes for color do not occupy the same locus in a chromosome; therefore, they are not allelomorphs.

Another example will help to distinguish between dominance and epistasis and between recessiveness and hypostasis. The Barred Plymouth Rock carries the gene *B* for barring and the gene *E* for the extension of black pigment to all parts of the plumage. *B*, barring, is dominant to *b*, nonbarring, as explained in the previous chapter; *B* and *b*, therefore, are genes that occupy the same locus in the chromosome. But *B* is epistatic to *E*, otherwise the bird would have solid black plumage; the gene *E* is prevented from expressing its effects in the presence of *B*. The gene *E*, therefore, is hypostatic to *B*, whereas *e* is recessive to *E*.

The White Plymouth Rock, as pointed out in the next chapter, carries the gene for barring, but it is not able to express itself because the genes for the production of pigment or coloring matter are absent. The gene for barring in the White Plymouth Rock is known, therefore, as a **cryptomere**.

Sometimes a new character appears unexpectedly in one generation and is transmitted through inheritance to succeeding generations. The new character is called a "**sport**" or a "**mutation**."

Old Ideas Discarded. Just as the most recent investigations of the inheritance of various characters have resulted in the development of new ideas concerning inheritance in general, so the newer knowledge has supplanted some of the old ideas once held concerning inheritance. Since some of these old ideas are still held by certain poultry breeders, a brief explanation is necessary to show why they are untenable.

Reversion, or the appearance of offspring resembling remote ancestors, has long been regarded by some poultry breeders to denote so-called impurity of breeding, but, as a matter of fact, it has a simple Mendelian explanation. In the next chapter it is observed that when a white variety, such as the White Dorking, is crossed with the White Silkie, the F_1 birds are colored, the males resembling males of the wild type, *Gallus bankiva*. Instead of there being impurity in either the

White Dorking or White Silkie to account for the results, it is pointed out that the White Dorking lacks a gene for the production of color which the White Silkie provides, and the White Silkie lacks the gene for the production of color which the White Dorking supplies. The term **reversion** has no standing in present-day discussions on inheritance.

Atavism has long been known as the phenomenon of resemblance of progeny to one or more of their grandparents but not to their parents. That this phenomenon is due to the segregation and recombination of genes has already been demonstrated, and numerous other illustrations are given in subsequent chapters.

Telegony is a term used with reference to the supposed influence of a previous mating on later offspring. A case is known of a poultry breeder who believed that if a Brown Leghorn male mated with a White Leghorn female, never again would the White Leghorn female produce purebred White Leghorn chicks when mated to a White Leghorn male. The origin of such a peculiar belief is probably due to the fact that in cases where a "foreign" male has mated with a female, eggs have been saved for hatching prior to the time that all the spermatozoa of the "foreign" male had perished, even though the female had later been mated with one of her own kind. At any rate, there is no such thing as telegony, as shown by the results secured in hundreds of cases.

The **inheritance of acquired characters** has been a subject of great controversy among plant and animal breeders for many years. A few breeders have claimed that a character acquired during the lifetime of the organism may be inherited, but the great majority have claimed that such is not possible. A good illustration of an acquired character in the case of the domestic fowl is the dubbed comb, that is, a comb that has been cut off. If dubbing were to be practiced on many successive generations of birds there is no reason to believe that the dubbed comb would be transmitted in inheritance, judging from the results secured with various animals in tests designed for the purpose of testing the validity of the theory of the inheritance of acquired characters.

Prepotency has long been regarded by practical poultry breeders as the ability of an individual to impress its characteristics upon its offspring to a much more marked degree than do other individuals. In some cases prepotency has been confused with dominance, as in the case of a White Leghorn being mated to a Barred Plymouth Rock or any other kind of colored bird. The progeny are not white because the White Leghorn had the stronger or more vigorous constitution but

because the gene responsible for the white of the White Leghorn is dominant to the gene for color. A black bird that is homozygous for black will produce nothing but black offspring when mated to a homozygous recessive white, like the White Minorca, whereas a black bird that is heterozygous for black will produce progeny consisting of one-half black and one-half white when mated to the same homozygous recessive white. The homozygous black bird is not more prepotent, in the sense in which it is usually used, than the heterozygous black bird but produces relatively twice as many black progeny because it has two genes for black instead of only one.

Present-day knowledge of inheritance teaches poultry breeders that they must look to the contents of the germ cells, the gametes, and not to the outward appearance, in order to ascertain the breeding value of a given bird.

THE INHERITANCE OF LINKED CHARACTERS

Two of the fundamental principles of Mendelian inheritance—dominance and the independent assortment of the genes—have been fully discussed in this chapter. Numerous illustrations involving both principles will be given in Chapters IV, V, and VI in the discussion of the inheritance of color and of morphological and physiological characters. Dominance and recessiveness have been shown to be clear-cut in many pairs of characters. The independent assortment of the genes has also been found to hold good in respect to many pairs of genes, giving the 3:1, the 9:3:3:1, and other ratios in the F_2 generations.

On the other hand, many cases have been established where independent assortment of the genes does not take place, so that in the F_2 generation a normal Mendelian ratio is not obtained. In several instances in the domestic fowl when parents differing in two pairs of characters have been crossed the F_2 generation, instead of consisting of a 9:3:3:1 ratio, contains an excess of birds having the same combination of characters as the original parents and a relatively small number of birds showing the new combination of characters.

The Principle of Linkage. These apparently abnormal F_2 ratios are due to the phenomenon known as linkage, which simply means that genes giving rise to certain characters tend to remain together instead of assorting themselves independently of each other when the gametes from the two sexes unite. For instance, if genes *A* and *B* are completely linked so that they never separate, different

results are produced in the F_2 generation from those which would be obtained if *A* and *B* separated freely, as shown in Fig. 26.

The cases of linkage that have been investigated in the domestic fowl have shown that linkage is rarely complete but is usually partial, that is, a given pair of genes tend to remain together but do separate to a certain extent, although less frequently than in the case of independent assortment.

	Independent Assortment of A and B	Complete Linkage of A and B
Parents	AABB x aabb	(AB)(AB) x (ab)(ab)
P_1 Gametes	AB ab	(AB) (ab)
F_1 Zygotes, ♂ and ♀	AaBb	(AB) (ab)
F_1 Gametes (formed in equal numbers)	♂: 1 AB, 1 Ab, 1 aB, 1 ab; ♀: 1 AB, 1 Ab, 1 aB, 1 ab	♂: 1 (AB), 1 (ab); ♀: 1 (AB), 1 (ab)
F_2 Zygotes (♂ + ♀)	1 AABB, 2 AABb, 2 AaBB, 4 AaBb = 9 AB; 1 AAbb, 2 Aabb = 3 Ab; 1 aaBB, 2 aaBb = 3 aB; 1 aabb = 1 ab	1 (AB)(AB), 2 (AB)(ab) = 3 AB; 1 (ab)(ab) = 1 ab

FIG. 26. Showing the difference in the results secured in the F_2 generation when two genes show independent assortment in one case and complete linkage in the other case. In the case of the independent assortment of *A* and *B*, similar results would be secured if the original cross was *AAbb* × *aaBB* instead of *AABB* × *aabb*, shown above.

When *A* and *B* exhibit partial linkage, the proportion of birds in the F_2 progeny having the same combination of characters as the parents and those having the new combinations of characters varies according to the way the original cross is made. If the original cross is of the nature *AABB* × *aabb*, each F_1 individual is of the constitution *AaBb* and forms the four kinds of gametes *AB*, *Ab*, *aB*, and *ab*, but the two parental combinations, *AB* and *ab*, are more numerous than the new combinations, *Ab* and *ab*. If the original cross is of the nature *AbAb* × *aBaB*, each F_1 individual is of the constitution *AaBb* and forms the four kinds of gametes *AB*, *Ab*, *aB*, and *ab*, but the two parental combinations, *Ab* and *aB*, are more numerous than the new combinations *AB* and *ab*. In the first cross, *AB* and *ab* are more numerous than *Ab* and *aB*, whereas in the second cross *Ab* and *aB* are

more numerous than *AB* and *ab*. Different results are secured depending upon the way the original cross is made, as shown in Fig. 27.

Owing to the fact that some characters are dominant over others, the F_2 ratio does not give a direct index of the kinds of gametes produced by the birds of the F_1 generation in cases of linkage. But a backcross of an F_1 bird heterozygous for each of two pairs of genes to the parent with both pairs of genes in a homozygous recessive condition provides an accurate index of the constitution of the gametes of the heterozygous F_1 bird.

The Principle of Crossing-Over. Genes that are located in the same chromosome, whether it be autosome or sex chromosome,

	When A and B enter the original cross together	When A and B do not enter the original cross together
Parents	(AB)(AB) x (ab)(ab)	(Ab)(Ab) x (aB)(aB)
P_1 Gametes	(AB) (ab)	Ab aB
F_1 Zygotes, ♂ and ♀	(AB) (ab)	(AB) (ab)

F_1 Gametes (formed in unequal numbers)	♂	♀	♂	♀
	+ 1 (AB)	+ 1 (AB)	1 (AB)	1 (AB)
	1 (Ab)	1 (Ab)	+ 1 (Ab)	+ 1 (Ab)
	1 (aB)	1 (aB)	+ 1 (aB)	+ 1 (aB)
	+ 1 (ab)	+ 1 (ab)	1 (ab)	1 (ab)

FIG. 27. Showing different proportions of F_1 gametes formed by F_1 individuals when *A* and *B* enter the original cross together and when they do not enter the original cross together, partial linkage being involved in both cases.

should always be inherited together as linked genes if the chromosome remains intact in inheritance. But it has been observed previously that linkage is rarely complete, thus indicating that frequently the chromosome is not inherited intact. Investigational work has established the fact that the gametes go through various stages of development and division in order that a gamete from the male may unite with a gamete from the female. During at least one of these stages of development each pair of chromosomes in a gamete lie side by side or even coil around each other and, occasionally, instead of separating intact, both chromosomes may break at the same place and the anterior portion of one chromosome of the pair becomes joined to the posterior portion of the other chromosome of the pair. This is supposed to give rise to an interchange of parts of the same pair of chromosomes; hence the suggestion that crossing-over takes place. The genes of one chromosome are said to cross over to the other chromosome of the pair, as illustrated in Fig. 28.

Suppose that the genes *A* and *B* from one parent enter into an original cross and that they are located at opposite ends of the same

chromosome. Suppose also that the genes *a* and *b* enter the same cross from the other parent. An F_1 bird will have the constitution *AaBb*, and the genes *A* and *a* and *B* and *b* will be in the same relative positions in each chromosome of the same pair. If crossing-over takes place, then each of the newly formed chromosomes will have *A* and *b* and *a* and *B* instead of *A* and *B* and *a* and *b*. The combinations *A* and *b* and *a* and *B* are new, whereas *A* and *B* and *a* and *b* are the parental combinations.

On the other hand, if the genes *A* and *b* enter the original cross from one parent and *a* and *B* from the other parent and crossing-over takes place, then *A* and *B* and *a* and *b* are the new combinations and *A* and *b* and *a* and *B* are the parental combinations. The parental or original combinations are noncross-overs and the new combinations are cross-overs.

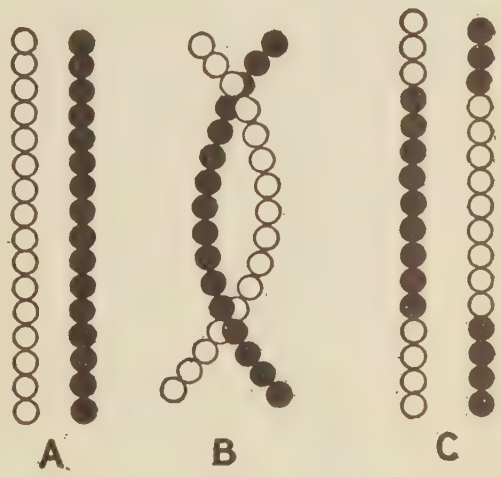

FIG. 28. Illustrating diagrammatically the manner in which crossing-over is supposed to take place. *A*, a pair of chromosomes composed of hypothetical genes. *B*, the pair of chromosomes in contact with each other at two places. *C*, the chromosomes have separated, each chromosome "breaking" at the points of contact with each other so that the genes of one chromosome have crossed over to the other chromosome. (After Agar, 1920, by permission The Macmillan Co.)

Determining Linkage Value. It has already been pointed out that if no crossing-over takes place linkage is complete, but that if crossing-over takes place linkage is not complete. It is obvious, therefore, that the amount of crossing-over that takes place is determined by the degree of linkage, or the degree of linkage is determined by the extent to which crossing-over takes place. Regardless of which is cause and which is effect, crossing-over is the corollary of linkage.

Each pair of linked genes exhibits a characteristic proportion of noncross-overs and cross-overs, the degree of linkage being determined in terms of the percentage of cross-overs in the gametic series. This is called the linkage value.

Under independent assortment the noncross-overs and cross-overs are approximately equal in numbers, whereas under linkage the noncross-overs are always more numerous than the cross-overs. Linkage may vary from slightly over 50 per cent to nearly 100 per cent noncross-overs of the total number of progeny. This is another way of saying that crossing-over may vary from about 50 per cent to less

than 1 per cent. In other words, linkage strength varies inversely as the cross-over value increases.

The degree of linkage which exists between any two genes is not influenced by the way in which the linked genes enter the cross. Suppose, for instance, that genes *A* and *B* exhibit 90 per cent linkage or 10 per cent crossing-over. Then the proportion of phenotypes in the F_2 generation of an original cross between a bird of the constitution (*AB*) and (*AB*) and one of the constitution (*ab*) (*ab*) can be predicted in advance. The F_1 birds from the original mating would be of the constitution (*AB*) (*ab*), and instead of producing a gametic ratio of equal numbers of *AB*, *Ab*, *aB*, and *ab*, expected under independent assortment of *A* and *B*, they would produce gametes in the following proportions:

45 per cent *AB*
45 per cent *ab* } 90 per cent linkage or noncross-overs

5 per cent *Ab*
5 per cent *aB* } 10 per cent cross-overs.

The results that would be secured in the F_2 generation produced by the F_1 birds of the constitution (*AB*) (*ab*), the genes *A* and *B* having entered the cross from the same parent, mated among themselves can be predicted in advance. In case of independent assortment of two pairs of genes an F_2 phenotypic ratio of 9 *AB*:3 *Ab*:3 *aB*:1 *ab* is produced, since the gametes *AB*, *Ab*, *aB*, and *ab* are produced in equal numbers by both the male and the female F_1 birds of the constitution *AaBb*. In 90 per cent linkage or 10 per cent crossing-over, the F_1 gametes (*AB*) and (*ab*) are each 9 times (45 as to 5) as numerous as the gametes (*Ab*) and (*aB*), so that the F_2 phenotypic ratio is quite different from that produced under independent assortment of the genes. A still different F_2 phenotypic ratio is produced in the case of 90 per cent linkage or 10 per cent crossing-over when the genes *A* and *B* enter the original cross from different parents, (*AA*) (*bb*) being mated to (*aa*) (*BB*).

The results in the F_2 generation can be predicted for any cross involving linkage, provided the linkage value is known, the linkage value being most readily determined by backcrossing. It should be noted, however, that there are cases where certain genes affect the amount of crossing-over that takes place between other genes.

Double and triple crossing-over has been reported in poultry, in which cases the pair of chromosomes has broken twice and three times, respectively, instead of only once as in single crossing-over.

Mapping the Chromosomes. It has already been pointed out that the fact that linkage exists between any two genes demonstrates

that the two genes are in the same chromosome. In general, the greater the distance between any two genes, the greater is the tendency for crossing-over to take place. Conversely, the closer together the two genes, the less liability is there of crossing-over taking place, or in other words, the greater is the linkage strength. The distance between two genes is determined by the crossing-over percentage, the distance being expressed in terms of units.

When it has been determined that there are three or more genes located in the same chromosome, their relative positions can be indicated according to the crossing-over percentages exhibited between each pair. Suppose, for instance, that genes *A*, *B*, *C*, and *D* are in the same chromosome, and that the crossing-over percentage for each of the pairs is as follows: *A* and *B*, 40; *A* and *C*, 20; *B* and *C*, 20; *A* and *D*, 10; and *C* and *D*, 10. Then it is apparent that *B* is four times as far from *A* as is *D*, that *C* is halfway between *A* and *B*, and that *D* is halfway between *A* and *C*. Such a procedure is called mapping the chromosomes. A few references to the detailed results secured from experimental matings will serve to demonstrate the principle involved in determining the relative distance apart of linked genes in a chromosome.

Suttle and Sipe (1932) established the fact that the genes for crest and for frizzled plumage are linked and, by determining the amount of crossing-over that takes place, were able to suggest the approximate distance separating these genes on the chromosome. Matings of heterozygous frizzle, crested males with normal females and matings of normal males with heterozygous frizzle, crested females produced the following results:

	Normal Plumage		Frizzle Plumage		Total Gametes Tested	Total Cross-Overs	Percentage of Crossing-Over
	Noncrested	Crested	Noncrested	Crested			
Observed	122	40	50	104	316	90	28.4
Expected	79	79	79	79	——— *without linkage* ———		

It should be noted at this time that the "Expected" results are based on the assumption of nonlinkage or independent assortment of the genes for crest and for frizzled plumage, but the results obtained show that these genes are linked together in the chromosome, approximately 28 units apart. Warren and Hutt (1936) also secured results showing linkage between the genes for crest and frizzled plumage. Their data added to that of Suttle and Sipe show that among a total of 677 gametes tested, there were 199 cross-overs, giving a crossing-over percentage of 29.4.

Warren and Hutt (1936) have submitted evidence of linkage among

the genes for crest, the dominant white plumage of the White Leghorn, and frizzled plumage. From matings made to determine the linkage value between the genes for crest and dominant white, the following results were secured:

White Plumage		Colored Plumage		Total Gametes Tested	Total Cross-Overs	Percentage of Crossing-Over
Crested	Noncrested	Crested	Noncrested			
572	85	70	569	1,296	155	12

Data from other matings made by Warren and Hutt when added to the above show that out of a total of 1,984 gametes tested there were 248 cross-overs, giving a crossing-over percentage of 12.5. From matings made to determine the linkage value between the genes for dominant white and frizzled plumage the following results were secured:

White Plumage		Colored Plumage		Total Gametes Tested	Total Cross-Overs	Percentage of Crossing-Over
Frizzled	Nonfrizzled	Frizzled	Nonfrizzled			
369	60	79	325	833	139	16.8

Other data submitted by Hutt (1933) when added to those above show that out of a total of 1,105 gametes tested there were 189 cross-overs, giving a crossing-over percentage of 17.1.

Landauer (1933) has submitted evidence indicating linkage between the genes for frizzled plumage and rumplessness. Among 341 gametes tested, there were 130 cross-overs, giving a crossing-over percentage of 38.1.

Since it has been demonstrated that the genes for crest, dominant white plumage, and frizzled plumage are linked, it should be possible to determine which one of the three is located between the other two. As a matter of fact, the crossing-over percentages indicate that the genes for crest and frizzled plumage are farthest apart and that the gene for dominant white plumage lies between the other two, being 12.5 units from the gene for crest and 17.1 units from the gene for frizzled plumage. The gene for crest has previously been reported to be 29.4 units from the gene from frizzled plumage. The arrangement of these genes is as shown below, *F* being the symbol for frizzled plumage, *I* for dominant white plumage, and *Cr* for crest. The figures indicate the actual results secured from experimental matings. Since it has also been shown that the genes for frizzled plumage and rumplessness are linked and are 38.1 units apart, it is apparent that the gene for rumplessness must be 8.7 units apart from the gene for crest or that it must be on the other side of the gene for frizzled plumage than are the genes for crest and dominant white plumage. Since Landauer

(1933) found no linkage between the genes for crest and rumplessness, it is apparent that the gene for rumplessness is on one side of the gene for frizzled plumage and that the genes for crest and dominant white plumage are on the other side. In Fig. 29 *Rm* signifies rumplessness.

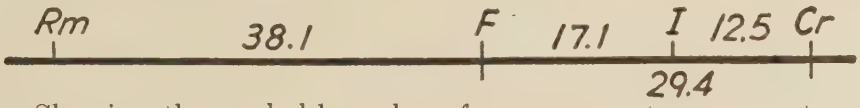

FIG. 29. Showing the probable order of arrangement on an autosome of the genes for rumplessness, *Rm;* frizzled plumage, *F;* dominant white plumage, *I;* and crest, *Cr;* together with the approximate distances they are apart as determined by the results of experimental matings. (After Hutt, 1936.)

Landauer (1932, 1933) reported the results secured from matings which demonstrated linkage between the genes for the Creeper condition and single comb. The results secured from backcross matings are reported as follows:

	Normal Condition		Creeper Condition		Total	Total	Percentage of
	Rose Comb	Single Comb	Rose Comb	Single Comb	Gametes Tested	Cross-Overs	Crossing-Over
Observed	3,577	11	17	3,703	7,308	28	0.38
Expected	1,827	1,827	1,827	1,827	——— *without linkage* ———		

The results secured from this experiment show that there is very close linkage between the genes for the Creeper condition and single comb, the crossing-over percentage being as low as 0.38 per cent. The genes involved are, therefore, close together on the chromosome.

The results of studies conducted by Taylor (1934) on linkage between the genes for Creeper and single comb, are in close agreement with those of Landauer. Taylor observed 0.59 per cent crossing-over in Creeper females and 0.40 per cent crossing-over in Creeper males. The results secured by Landauer and Taylor confirm the observation on linkage between these genes originally made by Serebrovsky and Petrov (1928), although their results indicated approximately 8 per cent crossing-over. Of the total number of 9,494 gametes tested by Landauer and Taylor there were 38 cross-overs, giving a crossing-over percentage of 0.4.

Hutt (1932) described a mutation of the uropygial gland, the dominant gene *U* causing the disappearance of the gland. *Uu* birds have two uropygial papillae and *uu* birds have one normal papilla. Hutt (1936) observed a crossing-over percentage of 29.6 between the *U* and *Rp*, the genes for rose comb. The genes for Creeper, single comb, rose comb, and the uropygial mutation are linked together, the Creeper and comb genes being very close together, but which is nearest the uropygial mutant gene has not been determined.

The recessive gene which causes Silkie plumage and the dominant "flightless" gene reported by Warren (1932) have been found by Warren (1936) to be linked, the percentage of crossing-over amounting to 10. Hutt (1936) has stated that available evidence indicates that these two genes are independent of the crest-dominant-white-frizzled group of genes as well as of the Creeper-comb-uropygial group of genes.

Another linkage group of genes that has been identified includes the genes for pea comb, naked-neck, and "marbling," a recessive gene described by Hertwig (1933) as producing a color pattern in the down of chicks. Between the gene for pea comb and the gene for marbling, Hertwig reported 32.8 per cent crossing-over and between the gene for marbling and naked-neck, he reported 45.6 per cent crossing-over. Since both Hertwig (1933) and Warren (1933) have found that pea comb and naked-neck are inherited independently, the pea-comb and naked-neck genes are a considerable distance apart on the chromosome.

TABLE 8. CROSSING-OVER IN THE CHICKEN IN RELATION TO SEX
(Warren, 1939)

	Crossing-over in Females			Crossing-over in Males		
	Total Gametes	No. of Cross-overs	Percentage of Crossing-over	Total Gametes	No. of Cross-overs	Percentage of Crossing-over
Crest—Dominant White:						
Warren	1,268	160	12.3	2,278	280	12.3
Hutt	35	2	5.7	379	55	14.5
Total	1,303	162	12.4	2,511	317	12.6
Frizzling—Dominant White:						
Warren	315	62	19.7	1,222	224	18.3
Hutt	248	46	18.5	337	48	14.2
Total	563	108	19.2	1,559	272	17.4
Frizzling—Crest:						
Warren	584	173	29.6	1,087	301	27.7
Hutt	35	11	31.4	80	24	30.0
Suttle and Sipe	235	68	28.9	81	22	27.2
Total	854	252	29.5	1,248	347	27.8
Silkie—Flightless:						
Warren	1,079	125	11.6	580	71	12.2
Rose Comb—Creeper:						
Landauer	4,313	23	0.53	3,095	5	0.16
Taylor	683	4	0.59	1,500	6	0.40
Total	4,996	27	0.54	4,595	11	0.24

Crossing-over apparently is not influenced by sex, according to data reported by Warren (1939).

The largest group of linked genes includes the following seven sex-linked genes: barring, silver, slow feathering, head spot, light down, light iris, and the inhibitor of dermal and mesodermal melanic pigment. The dominant gene *B* is responsible for the barring of the Barred Plymouth Rock. *S* is the dominant silver gene, recessives having red, buff, golden, or black and golden plumage. The dominant gene for slow feathering, first reported by Serebrovsky (1922), is carried by practically all general-purpose breeds, whereas Leghorns and Anconas carry the recessive gene for rapid feathering. The head-spot characteristic has been reported by Hertwig (1930), chicks homozygous for this recessive gene having an irregular streak of dark pigment extending down the back of the head and along the neck. The head-spot character has been observed in Houdan and Golden-Spangled Hamburg chicks. The light-down character reported by Hertwig and Rittershaus (1929) is due to a dominant gene which inhibits brown pigment in the down of chicks that are not black. The light-iris condition is due to a dominant gene, reported by MacArthur (1933), birds carrying the recessive allele having brownish-black irises. The presence of dermal and mesodermal pigment gives rise to blue, slate, or willow shanks, whereas the presence of the sex-linked inhibitor prevents the expression of blue, slate, or willow shanks.

The amount of crossing-over that has been observed to take place between certain pairs of these sex-linked genes has been presented in tabular form by Hutt (1936) and is presented here for the sake of brevity. The symbols in Table 9 refer to genes for the following characters: *B* = barring, *S* = silver, *K* = slow feathering, *Ko* = head spot, *Li* = light down, *Br* = light iris, *Id* = inhibitor of dermal and mesodermal pigment.

Hutt (1936) has suggested that the probable order of arrangement of this group of seven genes on the sex chromosome is *Ko, Id, B, Br, Li, S,* and *K*. Hutt indicated, however, that a final decision on the arrangement must await further data on the arrangement of other genes with *Br* and with *Li* and the critical test of linkage between these two genes. Warren (1934) obtained results which indicate that the sex-linked gene for sexual maturity is located between the genes *B*, for barring, and *S*, for silver.

It is of great fundamental importance to be able to map the chromosomes as completely as possible because the greater the number of linkage groups established the greater is the possibility of determining the existence of linkage between the genes for egg production

Table 9. Crossing-over Percentages between Different Pairs of Sex-linked Genes

(Hutt, 1936)

Genes Tested	Investigator	Crossing-over Percentage
B and *S*	All	42 to 49
B and *K*	All	43 to 49
B and *Li*	Hertwig and Rittershans (1929) Hertwig (1930), average	39.4
Id and *Li*	Hertwig (1930)	30.5
K and *S*	All	8 to 14
K and *Li*	Hertwig and Rittershans (1929) Hertwig (1930), average	24
S and *Li*	Hertwig and Rittershans (1929) Hertwig (1930), average	15.7
Ko and *B*	Hertwig (1933)	13.5
Ko and *S*	Hertwig (1933)	50.2
Ko and *K*	Hertwig (1933)	47.3
Ko and *Li*	Hertwig (1930)	47
Br and *S*	MacArthur (1933)	43.8
Br and *K*	MacArthur (1933)	41.8
Br and *D*	MacArthur (1933)	27.5

and the genes for some of the color and morphological characters, the inheritance of which has been discussed in subsequent chapters. If it can be determined that certain of these visible characters are linked with egg production and other characters of economic importance, the task of the poultry breeder will be made much simpler.

PROBLEMS

1. What does mating accomplish?
2. What is the relation between gametes and zygotes?
3. What part do chromosomes play in inheritance?
4. Of what significance are genes?
5. What practical use can be made of sex-linked inheritance?
6. What is implied by the term "inheritance"?
7. Explain how variations that exist among domestic fowls are of value in studying the inheritance of characters.
8. State the derivation of each of the following terms and give an illustration of the proper use of each term: gene, gamete, genotype, phenotype, homozygous, heterozygous, monohybrid, F_1, F_2, allelomorph, lethal.
9. Of what value in studies on the inheritance of characters is the fact that certain characters show dominance over others?
10. What are the three major principles of inheritance established by the work of Mendel?
11. Make out a checkerboard scheme showing the zygotes produced in a cross between Black Single-Comb Bantams and White Rose-Comb Bantams, the

symbol *R* being used for rose comb and *r* for single comb, and *N* for the black plumage and *n* for white plumage.

12. The zygote of the Rose-Comb White Leghorn is represented by *RRII* and the zygote of the Single-Comb Black Leghorn is represented by *rrii*, rose comb being dominant to single comb and white being dominant to black, the white of the White Leghorn being due to a dominant gene *I*, which inhibits the development of color. What is the zygote of the F_1 generation and what are the genotypes and phenotypes produced in the F_2 generation?

13. What is the significance of the segregation and independent assortment of the genes in inheritance?

14. In what way may a knowledge of Mendelian inheritance be of value in practical poultry-breeding work?

15. Write a brief essay on Mendel's contribution to the science of breeding.

16. What is the relationship between linkage and crossing-over?

17. Outline a breeding project with a view to determining the linkage strength between two genes whose linkage strength has not yet been determined.

18. What is the relationship between two genes when (1) there is no crossing-over and when (2) there is 50 per cent crossing-over?

19. From the information given concerning the numbers of chromosomes in the domestic fowl, how many linkage groups should it be possible to establish in the case of the male and in the case of the female?

20. What are some of the practical aspects involved in linkage?

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CHAPTER IV

THE INHERITANCE OF COLOR CHARACTERS

Color characters in domestic fowls are among the most conspicuous of all the characters they possess and constitute the basis for differentiating the varieties of a breed. Color characters include the down color of chicks, adult plumage color, skin color, earlobe color, shank color, and egg-shell color, a discussion of the last character being reserved for the chapter devoted to the inheritance of egg characters. A review of the numerous investigations undertaken to determine the nature of the inheritance of these various color characters must of necessity be brief in a book of this kind.

In order that the poultry breeder may secure the most satisfactory results from his poultry-breeding operations he should know as much as possible concerning the genetics of the breed or variety in which he may be interested. A knowledge of the manner in which a certain undesirable character is inherited may enable him to eliminate it from his flock with comparative ease. Moreover, when one knows how various characters are inherited, breeding work becomes much more interesting and may be made much more profitable.

THE INHERITANCE OF WHITE PLUMAGE

In Chapter I mention is made of several white breeds and varieties as the White Leghorn, White Plymouth Rock, White Wyandotte, White Rose-Comb Bantam, and Silkie. The white of the White Leghorn is of the dominant type and most other white breeds and varieties apparently belong to one of four kinds of recessive whites. That there are at least two kinds of recessive whites is apparent from the fact that, when they are crossed, the progeny is colored, demonstrating that each kind of white lacked a gene for the expression of pigment that the other kind possessed. Other kinds of recessive whites include the "albino" observed by Warren (1933) and the red-splashed white mutation observed by Quinn (1934).

Down Color. Although the down color of the great majority of the chicks of all white breeds and varieties is pale yellowish cream, occasionally some chicks appear that are chalk white, smoky white, or reddish white.

Regarding the down color of the chicks of one of the recessive

white groups, Punnett (1923) points out that the chicks of the Silkie and White Rose-Comb Bantam differ somewhat in that in the Silkie the down color is yellowish cream with generally more or less buffish orange tinge on the dorsal surface, whereas in the White Rose-Comb Bantam the down color is creamy on the ventral and pale bluish on the dorsal surface.

The down color of the chicks of the other recessive white group is usually yellowish cream, though some of the chicks may be chalk white and sometimes, as Punnett (1923) points out, homozygous recessive whites may show an occasional black tick in the plumage.

Dominant White Plumage. Bateson (1902) demonstrated that the White Leghorn is white because of the presence of a gene which prevents the production of melanic pigment (black). Bateson's observation regarding the color-inhibiting nature of the gene in White Leghorns has been confirmed by Bateson and Punnett (1905, 1906), Hurst (1905), Davenport (1906), and Hadley (1913, 1914, 1915), who proved conclusively that the White Leghorn possesses a gene for the production of color, which, however, does not find expression because of the presence of the inhibiting gene, the symbol for which is *I*. Gortner (1910) found that the dominance of white in the White Leghorn is due to the presence of an enzyme, which prevents the development of color.

When a White Leghorn, either male or female, is mated with a colored bird, such as Black Minorca, the F_1 chicks are white, except that many of the chicks may have black spots in the down. These chicks with black ticking usually develop into adults having some black in their plumage, the partially black feathers exhibiting barring except in the case of F_1 females secured from a cross of a colored male and a White Leghorn female. The dominant inhibiting gene, *I*, has also been reported to be present in certain White Minorcas and White Plymouth Rocks, although the results of the great majority of investigations concerning the inheritance of white plumage in these two varieties have shown that white is recessive to color. The strains of White Minorcas and White Plymouth Rocks which were found to carry the dominant white may have resulted from previous crossings of these varieties with White Leghorns. Even if such crossings had been made and the progeny invariably conformed to the breed type and color standard of the White Minorca and White Plymouth Rock, the progeny in each case might well be regarded as White Minorcas and White Plymouth Rocks.

Punnett (1923) points out that in England breeders of White Wyandottes have sometimes used White Leghorns in their matings,

but so long as the progeny of such matings are of the Wyandotte shape and have rose combs they are regarded by the poultry breeders as being White Wyandottes.

That the dominant inhibiting gene is not completely dominant in the case of certain crosses is shown by the appearance of partially colored F_1 birds in certain matings. Jull and Quinn (1931) have observed that, in reciprocal matings between White Leghorns and Partridge Plymouth Rocks, a number of F_1 adult males have red shoulders and some red over the back and some of the F_1 adult females have a reddish cast on the underside of the throat and over the breast. Serebrovsky (1926) states that the inhibiting gene of White Leghorns inhibits the development of all color except the red color of the shoulders, back, hackle, and saddle of the male. Warren (1930*a*) concluded that the salmon-breast condition in a strain of White Leghorn females is due to a single gene, which behaves as a recessive toward the white of the White Leghorn. Danforth (1933) has shown that *I* is not very effective in suppressing yellow color, and in birds homozygous for yellow the white may be hypostatic and fail to appear. Fisher (1934) and Brandt (1936) have shown that when *I* is in a heterozygous condition it is not completely dominant to color. *I*, therefore, may be regarded as an autosomal gene almost completely dominant to color.

Recessive White Plumage. It has already been shown that when the White Rose-Comb Bantam is crossed with a colored bird the progeny is colored, demonstrating the recessive nature of the white in the White Rose-Comb Bantam. Likewise, when the White Dorking, White Wyandotte, or any other white except the White Leghorn is crossed with a colored bird, the progeny is colored.

It might be assumed, therefore, that the recessiveness of these various recessive white breeds and varieties is of the same nature, but such is not always the case. When Bateson and Punnett (1906) crossed a White Silkie with a White Dorking the F_1 progeny was colored and the F_2 progeny consisted of the proportion of 9 colored to 7 white. These results show that each of the white parents lacked a gene for the expression of pigment which the other possessed. In one sense, the two recessive whites are complementary, that is, one gene supplies what the other lacks, so that when they are brought together it is possible for pigment to be expressed.

For some time it was supposed that the White Silkie and the White Rose-Comb Bantam belonged to one group of recessive whites and that practically all other recessive white breeds and varieties belonged to another group. Quinn and Godfrey (1937) have shown, however, that

the White Silkie and White Rose-Comb Bantam stock used in their experimental matings had the same kind of recessive white as the other white recessive breeds and varieties with which they experimented.

The F_2 generation secured from an original mating of White Silkies with colored birds consisted of 1,748 colored and 606 white chicks, the ratio of colored to white being approximately 3:1. Backcross matings of White Silkies and F_1 colored birds produced 715 colored and 717 white chicks, almost exactly a 1:1 ratio. The F_2 generation secured from an original mating of White Rose-Comb Bantams with colored birds consisted of 91 colored and 35 white chicks, approximately a 3:1 ratio. Backcross matings of White Rose-Comb Bantams and F_1 colored birds produced 67 colored and 65 white chicks, a 1:1 ratio. Quinn (1936) showed that white progeny only was produced by mating White Silkies to White Rose-Comb Bantams, White Silkies to White Wyandottes, and White Rose-Comb Bantams to White Wyandottes. It would appear, therefore, that these White Silkies and White Rose-Comb Bantams were of the same nature, as far as recessiveness of white is concerned, as the larger white recessive breeds and varieties. It is apparent that the recessiveness of the Bateson and Punnett White Silkies is of a different order from the recessiveness of the Quinn and Godfrey Silkies.

It has been suggested that the difference between the one group of recessive whites, represented by the Bateson and Punnett White Silkies, and the other groups of recessive whites is of a chemical nature, the gene of one group producing an oxidase and the gene of the other group producing chromogen, so that the two when combined give rise to the production of pigment.

A ratio of 9 colored to 7 white birds is obtained in the F_2 generation whenever the gene *C*, representing chromogen, and the gene *O*, representing oxidase, are brought together. The 16 zygotes consist of

1 *CCOO* 2 *CCOo* 2 *CcOO* 4 *CcOo*	9 containing both *C* and *O*	9 colored birds
1 *CCoo* 2 *Ccoo*	3 containing *C* but not *O*	7 white birds
1 *ccOO* 2 *ccOo*	3 containing *O* but not *C*	
1 *ccoo*	1 containing neither *C* nor *O*	

All colored birds, of course, contain both *C* and *O*. The fact that

the Quinn and Godfrey White Silkies and White Rose-Comb Bantams gave F_2 ratios approximating 3:1 when these birds were mated to colored birds shows that there was only one gene difference between these recessive whites and the colored birds. The same is true of other recessive whites such as White Dorkings, White Minorcas, and White Wyandottes. By making appropriate critical tests between White Silkies and White Rose-Comb Bantams on the one hand and White Wyandottes and White Plymouth Rocks on the other hand, Quinn (1936) has shown that they do not differ in the nature of their white recessiveness. As far as recessiveness of white is concerned, they are supposed to be of the genetic constitution *ccOO*. On the other hand, the genetic constitution of the other type of recessive white represented by the Bateson and Punnett White Silkie is supposed to be *CCoo*.

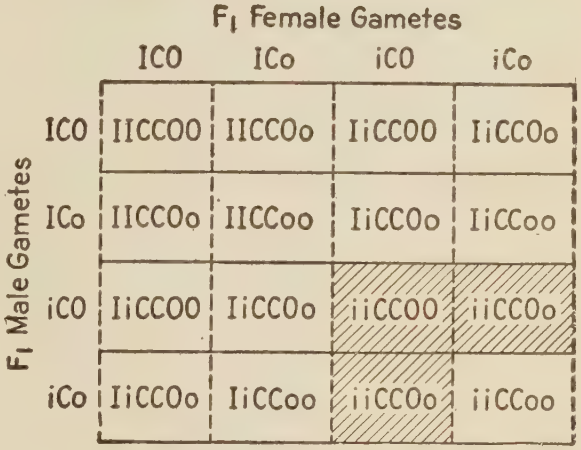

FIG. 30. The F_2 generation secured from an original cross between a dominant white, the White Leghorn, and a recessive white, the White Silkie, consists of 13 white to 3 colored birds. The gene I inhibits the development of color but where it is not present both C and O must be present in order that color may be produced.

Crew (1933) has shown that some Wyandottes with which he experimented carried genes for black and for barring, white plumage being exhibited because of the lack of the chromogen-producing gene *C*. Quinn (1936) has shown that several recessive white breeds and varieties may carry genes, as cryptomeres, which are responsible for specific colors and patterns. Since the albino white observed by Warren (1933) is a recessive, the gene responsible for this character is designated *a*. In a certain strain of Rhode Island Reds, Quinn (1934) reported the appearance at hatching time of some white chicks, most of which had a red spot on the head. The adult plumage of these chicks was white with varying amounts of red feathers over the body. This white-plumage mutation is recessive and is differentiated from the Rhode Island Red by the autosomal gene *p*, which for the most part inhibits the expression of pigment. Quinn (1935) found that the *P* gene tends to suppress the columbian pattern. Quinn (1938) records that white chicks with red head spots have been secured, about 74 per cent of which were males and 26 per cent females. Chicks having one red head spot were about equally divided as to sex; among the chicks with two or more red head spots, there were approximately

twice as many females as males. Thus, the red head spotting of chicks in relation to sex in Red-Splashed Whites is similar to black head spotting of chicks in relation to sex in Rhode Island Reds.

Present-day knowledge of the inheritance of white plumage indicates that the different kinds of white may be designated as follows:

Dominant white as in White Leghorns	*IICCOOPPAA*
Recessive white (nonchromogen) as in White Wyandottes, White Minorcas, etc.	*iiccOOPPAA*
Recessive white (nonoxidase) as in some White Silkies (Bateson and Punnett, 1906)	*iiCCooPPAA*
Recessive white (nonpigment) as in Red-Splashed Whites (Quinn, 1934)	*iiCCOOppAA*
Recessive white as in albinos (Warren, 1933)	*iiccOOPPaa*

The foregoing discussion on the inheritance of white plumage makes it clear that such a simple character has a rather complex background.

INHERITANCE OF BLACK PLUMAGE

Black breeds and varieties are very numerous; they include Jersey Black Giants, Black Sumatras, Black Hamburgs, Black Langshans, Black Leghorns, Black Minorcas, Black Orpingtons, Black Wyandottes, Black Rose-Comb Bantams, and others.

Down Color. The down color of the chicks of all black breeds and varieties is black, except that there is usually a variable amount of white or gray on the ventral surface. Quinn and Knox (1940) observed that it was not possible to segregate the chicks at hatching time according to sex on the basis of down, shank, or beak color with an accuracy above about 58 per cent.

How Black Behaves in Inheritance. Black is recessive to the white of the White Leghorns. Crosses made by Davenport (1906) and Hadley (1914) between black and recessive white varieties have shown that black is dominant.

In a cross between Black Langshans and Brown Leghorns made by Punnett and Bailey it is reported by Punnett (1923) that the F_1 chicks were black and that as adults the pullets were full black, whereas the cockerels were black with some gold in the hackles and on the shoulders. "In the F_2 progeny the black and the brown striped downs segregated cleanly, giving a simple 3:1 ratio." Punnett adds that the results of this cross suggest that brown is differentiated from black by a single gene and that there are various forms of brown which can be transformed into black by the addition of this gene.

In black breeds and varieties the melanic pigment is distributed evenly to all parts of the plumage, and from crosses between Black Orpingtons and Light Bantams, which have black restricted to the neck, wings, and tail, Dunn (1922*a*, 1923) has suggested that black breeds and varieties contain a pair of genes, designated *EE*, for the extension of the black or melanic pigment. Dunn used the symbol E^m, but since he refers to the same gene as other investigators who have investigated the inheritance of black plumage and since they have used the symbol *E* to denote the gene having the same effect as Dunn's E^m gene, the symbol *E* only is used in this discussion. That the Black Langshan carries *EE* has been demonstrated by Lippincott (1923), Serebrovsky (1926), and Knox (1927), and Serebrovsky (1926) also showed that *EE* is present in Black Minorcas and Black Orpingtons.

Occasionally the inheritance of black cannot be interpreted on a monohybrid basis, a case in point being a cross reported by Punnett (1923) between Black Langshans and Golden-Penciled Hamburgs. The F_1 chicks were all black, and as adults the females were solid black and the males were black with some gold in the hackles. The F_2 progeny consisted of 113 blacks and 80 nonblacks, which is very close to a 9:7 ratio (108.56:84.42). This suggests the inheritance of black in this particular cross on a dihybrid instead of a monohybrid basis. Moreover, F_1 birds backcrossed to Golden-Penciled Hamburgs produced 29 blacks and 92 nonblacks, expectation being one-fourth blacks in the total progeny or a proportion of 30.25 blacks to 90.75 nonblacks. It is quite evident, therefore, that the Golden-Penciled Hamburg lacks two genes necessary for the extension of black pigment.

THE INHERITANCE OF BUFF PLUMAGE

Buff varieties are numerous and include Buff Brahmas, Buff Cochins, Buff Leghorns, Buff Orpingtons, Buff Plymouth Rocks, Buff Wyandottes, and others. Foreign color, including black, in any part of the plumage is regarded by poultry breeders as a serious defect. At the same time, it is well known that black in varying amounts is sometimes present in the feathers of the neck, wings, and tail. Because of this condition, Dunn (1923) has suggested that buff is in reality a pattern.

Down Color. The down color of the chicks of buff varieties is buff, often varying from a very light to a very dark shade, and frequently being of a lighter shade on the ventral than on the dorsal surface.

How Buff Behaves in Inheritance. Comparatively few experiments have been conducted with the view of determining the nature of the inheritance of buff, but the results of crosses made in recent years suggest that the situation is more complicated than was originally supposed.

The results of a cross of Buff Cochins × Black Hamburgs made by Hurst (1905) and of a cross of Black Cochins × Buff Cochins made by Davenport (1909) indicate that buff is recessive to black.

The results secured from reciprocal crosses between Buff Orpingtons and Light Brahmas, which have what is called the "columbian color pattern" as found in Columbian Plymouth Rocks and Columbian Wyandottes, led Dunn (1922*a*, 1922*b*, 1923) to conclude that "buff and columbian colorations of fowls differ in one principal gene determining the presence or absence of buff in the plumage and probably in multiple factors (genes) determining the amount of black developed in wing, tail and hackle feathers." In connection with this discussion concerning the relationship between buff color and the columbian pattern, Warren (1928*a*) states that the Buff Leghorn carries the columbian pattern, in which black pigment is restricted to the neck feathers, tail, and portions of the wings.

Dunn (1923) concluded that buff differs from black by a gene determining the restriction of black to the hackle, tail, and wings. The dominant allelomorph of this gene is present in self-blacks, as previously observed under the discussion of the inheritance of black, where it was pointed out that *EE* effects the extension of black pigment to all parts of the plumage. According to Dunn, therefore, black fowls are genetically buffs with the extension gene superimposed, buff varieties carrying *ee*.

Knox (1927) made reciprocal crosses between Buff Orpingtons and Black Langshans and secured F_1 blacks only, except that there was a slight amount of buff across the wings and back and in the neck, thus showing that buff is in general recessive to black. Knox also crossed Buff Orpingtons and White Plymouth Rocks reciprocally, and the buff color appearing in all F_1 hybrids showed buff to be dominant to the recessive white.

Knox found that the results he secured could be interpreted only on the assumption of there being two genes responsible for the development of buff color, each producing the same effect, and that there is an interaction between these genes for buff and the genes *C* and *E*, depending upon whether either one or both is in a homozygous condition. Knox has designated the symbols *Bu Bu* and *Bu' Bu'* to represent the two pair of buff-producing genes, their respective allelomorphs being *bu bu* and *bu' bu'*.

The results which Knox secured in his F_2 and backcross generations led him to make the following assumptions: buff is epistatic to black when three or four genes for buff are in the presence of *CC* and *EE*; buff is epistatic to black when three or four genes for buff are in the presence of either *Cc* and *EE* or *CC* and *Ee*; buff is epistatic to black when two or more genes for buff are in the presence of *Cc* and *Ee*.

Although relatively few experiments have been conducted involving the inheritance of buff plumage, the results secured indicate that buff color or buff "pattern," if such there be, rests upon a complex genetic basis, and much further work seems necessary to test the validity of the hypotheses put forward.

THE INHERITANCE OF BLUE PLUMAGE

There is one blue breed, the Blue Andalusian, and a few blue varieties, including Blue Leghorns, Blue Orpingtons, and Blue Plymouth Rocks.

Down Color. The down color of the chicks of the blue breed and varieties is an even shade of slaty blue, except that the breast and ventral surface of the body are lighter, approaching bluish white.

Blue a Heterozygous Color. The results secured from matings of Blue Andalusians represent the classical example of the peculiar mode of inheritance in all blue varieties and are in marked contrast to the results secured from matings of all other breeds and varieties.

A mating of Blue Andalusian males to Blue Andalusian females does not produce all Blue Andalusians, for if large enough numbers of progeny are produced one-fourth are black, one-fourth are white with a few blue feathers, and one-half are typical Blue Andalusians. In other words, the Blue Andalusian does not breed true.

Bateson and Punnett (1906) made all possible types of matings between each two of the three different colors—blacks, blue-splashed whites, and blues—and found that the blacks are the blue-splashed white breed true, whereas the blues were heterozygous in that they invariably produce progeny in the ratio of 1:2:1, that is, 1 blue-splashed white to 2 blues to 1 black.

Hagedoorn and Hagedoorn (1914) crossed a Blue Andalusian with a recessive white and secured equal numbers of blue and black progeny.

Concerning the genes responsible for the development of blue plumage, Lippincott (1918, 1921, 1923) proposed the theory that two genes are involved, the dominant condition of both never being present in the same gamete. Punnett (1923) points out, however,

that Blue Andalusians are fundamentally a black breed and that the blue-splashed white birds and blue birds result from the operation of a gene which partially inhibits the production of pigment, the inhibiting gene being in a homozygous dominant condition in the blue-splashed white birds and in heterozygous condition in the blue birds. The inhibiting gene would naturally be entirely lacking in the black birds. Serebrovsky (1926) mentions the same gene for blue which inhibits black and calls it "todi."

Punnett's interpretation of the situation explains in a satisfactory manner the results secured from the various matings among the three kinds of Andalusians as well as between each of the three kinds of Andalusians and recessive whites.

It should be pointed out, however, that the gene which partially inhibits the development of black pigment in blue-splashed white and Blue Andalusians is not the same gene which inhibits the development of pigment in White Leghorns.

THE INHERITANCE OF "RED" PLUMAGE

So far as is known the Red Leghorn is the only variety that is red in all parts of its plumage, although from the standpoint of inheritance "red" is also understood to mean the color found in Rhode Island Reds, New Hampshires, and Black-Tailed Red Leghorns, a variety of Leghorns developed recently. The plumage color is a rich, brilliant red with the exception that there is black in the wings and tails of both sexes and in the hackle of the males and frequently in the neck feathers of the females.

Down Color. The down color of the chicks of these "red" breeds and varieties varies considerably in the shade of red. The lightest chicks are cream colored, with perhaps but a tinge of red, whereas the darkest chicks are a chocolate brown. Frequently the ventral surface is of a lighter shade of red than the dorsal surface and occasionally dark striping is present.

Warren (1929) made a comprehensive study of down color in Rhode Island Red chicks by developing by selection a light-colored-down strain and a dark-colored-down strain, after which the two strains were crossed, the results indicating that neither shade is dominant.

Byerly and Quinn (1936) made the interesting observation that the sex of Rhode Island Red chicks can be distinguished at hatching time with a reasonable degree of accuracy by an examination of the down color. Quinn and Byerly (1937) confirmed their original observation with other strains of Rhode Island Red chicks and found that it

also applied to New Hampshire chicks. Female chicks for the most part had either a black spot at the base of the head or black striping on the head and along the back or both, whereas male chicks, for the most part, were free of both black spotting and striping. The authors suggest that the results might be accounted for on the basis of two or more genes affecting spotting and striping at least one of which is sex-linked, in accordance with the suggestion of Rittershaus (1930), or the results might be due to sex-limited inheritance by the action of the female sex hormone. The final solution of the problem has not been attained. Hays (1939) observed that about 63 per cent of the chicks with no pigmented areas were males and that about 46 per cent of the female chicks had pigmented areas. Down pigmentation, however, was found not to be intimately associated with adult plumage color.

Adult Plumage. Ladebeck (1922) investigated the pigment of Rhode Island Red feathers and observed that the red feathers contain reddish-brown or reddish-yellow pigment globules of melanic nature and that the black feathers contain rod-shaped and elliptical-shaped black pigment granules of varying sizes.

Dunn (1922*b*) observed that Rhode Island Reds are recessive to *E*, the gene for the extension of black pigment to all parts of the plumage. Rhode Island Reds, therefore, carry *e*, which restricts the black to the neck, wings, and tail, as in the case of Light Brahmas and other varieties with the columbian pattern. The results secured by Hays (1926) led him to conclude that three genes are chiefly concerned in the development of Rhode Island Red plumage color. On the other hand, Warren and Gordon (1934), although securing evidence concerning the heritability of the variations in intensity of pigmentation of the general surface, hackle, and breast, concluded that several genes are involved.

THE INHERITANCE OF "BLACK-RED" PLUMAGE

The Modern Black-Breasted Red Game is a typical example of the so-called "black-red" breeds and varieties. As the name suggests, there is a mixture of black plumage and red or shades of red plumage. In the male the front of the neck, the breast, the shoulders, practically all the primaries and part of the secondaries, the body, and the tail and tail coverts are black, whereas the hackle and saddle are bright red. In the female the neck is light golden, each feather having a black stripe through the middle; the front of the neck and the breast are salmon colored; the primaries and main tail feathers, except the two top ones, are black, and the rest of the plumage is ashy

brown, that over the shoulders and the wing-bows and the secondaries being stippled with golden brown.

The Single-Comb Brown Leghorn is another black-red variety, the color pattern being somewhat the same as in the Modern Black-Breasted Red Game. *Gallus gallus bankiva* is of the same general color pattern.

Very little is known concerning the inheritance of the "black-red" plumage pattern although the results of a few experiments lead to interesting observations regarding the relationship between black-reds and blacks and between black-reds and varieties like the Silver-Gray Dorking, the Silver Duckwing Game, and the Dark Dorking, varieties in which the females have stippled plumage.

In a cross between Brown Leghorns and Black Langshans, Punnett (1923) found that the F_1 females were completely black and the F_1 males were black with some gold in the hackles and on the shoulders. This is not a case of sex-linked inheritance, because the same results were obtained from reciprocal crosses. Apparently one or more genes are involved which are responsible for the development of gold in the hackle and on the shoulders of the males, and except for this difference it is apparent, as Punnett has suggested, that the Brown Leghorn can be transformed into a black bird by the addition of the gene *E* for the extension of black pigment.

THE INHERITANCE OF THE RED PYLE PATTERN

The color of the Red Pyle Game involves a very interesting though complex problem concerning the nature of the inheritance of certain colored sections of the plumage. Both sexes are for the most part white. The male has a considerable amount of orange and red feathers on his dorsal side as follows: the neck and hackle feathers are light orange, the wing-bows are red; the outer webs of the lower primary feathers are bay colored; part of the outer web of the secondaries are red; the feathers over the back are red and the saddle feathers are light orange. In the female, except for the white neck feathers being edged with gold, the only section having colored feathers is the front of the neck, where the feathers are white tinged with salmon.

Hurst (1905) and Davenport (1906, 1909) crossed buff varieties with the White Leghorn, the F_1 birds being somewhat like pyle birds in plumage color. Punnett (1923) points out that the Red Pyle Game can produce black-reds, the white of the Red Pyle Game being dominant to the melanic ground color of the black-red. Cunningham (1919), however, has shown that the white plumage of a Red Pyle

may be of the nature of a recessive white, since he was able to produce pyle-colored fowls from a cross between the Junglefowl and the White Silkie.

Punnett (1923) states that the orange-red pattern of the Red Pyle Game behaves as a distinct plumage character and may be associated with different ground colors, and that "it is neither inhibited by the dominant white nor prevented from making its appearance when some constituent for the development of the melanic pigment is absent, as in recessive whites of the Silkie types." The fact that Davenport (1909) secured pyle-colored birds in the F_2 generation from a White Leghorn $\times$ buff cross led Punnett to suggest that the orange-red color in the dominant white bird is inhibited by the presence of a gene for "silver." The fact that the White Leghorn possesses the gene for silver has been demonstrated by various workers, as pointed out later.

Serebrovsky (1926) suggests that the gene which he calls "tule" is responsible for the development of the red in the shoulders, back, saddle, and hackle feathers in the male.

THE INHERITANCE OF MOTTLING

The Mottled Ancona and Mottled Houdan have what is known as mottled plumage, in which the ground color is black, a variable portion of the black feathers in different sections of the bird being tipped with white.

Down Color. The down color of Mottled Ancona chicks is black on the dorsal surface and creamy yellow shading to white on the lower part of the head, the breast, and ventral surface. The down color of Mottled Houdan chicks is black on the dorsal surface and on the sides of the body, including the outer thighs, whereas the crest, throat, breast, and fluff are lemon yellow.

How Mottling Behaves in Inheritance. Both Hurst (1905) and Davenport (1906) crossed the Mottled Houdan with the White Leghorn and each secured an F_2 generation indicating that mottling behaves as a simple Mendelian recessive to the white of the White Leghorn. Davenport (1906) also crossed the Mottled Houdan with the Black Minorca and observed that the F_1 birds were almost completely black, the black of the Minorca being dominant to mottling. Apparently no F_2 generation was raised.

Serebrovsky (1926) observed that the mottling of the Mottled Orloff is recessive to solid color but differs from the mottling of the Mottled Houdan, since the crossing of Mottled Orloffs and Houdans produced self-blacks.

Asmundson and Milne (1930) made crosses between Mottled Anconas and each of the following colored varieties: Black Minorcas, Black Orpingtons, and Buff Wyandottes. The crosses between Mottled Anconas and Black Minorcas and Black Orpingtons produced F_1 birds that were entirely black and F_2 birds consisting of 45 black and 14 mottled ones, the expected ratio on a monohybrid basis being 44.25 blacks to 14.75 mottled ones. The results of the F_1 and various backcross matings indicate that mottling is recessive to self-color on a monohybrid basis.

The results which Asmundson and Milne secured when Mottled Anconas were crossed with Buff Wyandottes led them to conclude that Mottled Anconas carry *EE*. The results they secured between Mottled Anconas and Black Minorcas and between Mottled Anconas and Black Orpingtons led them to conclude that Mottled Anconas carry a pair of genes, *e'e'*, whose presence is responsible for the appearance of the white tips on some of the feathers.

THE INHERITANCE OF PIED PLUMAGE

What is known as pied plumage is found in Exchequer Leghorns and is characterized by a mixture of black and white. In the male the neck and hackle feathers are black or mostly black, each feather having a streak of white down the center; the breast, wing-bows, and thighs are white evenly mottled with black; the main sickle feathers are white, whereas the tail and saddle feathers are black with white markings. In the female the ground color is white, many of the feathers being marked with black concentric spots, the general appearance of the female being much like that of the male.

Apparently the chief differences between pied and mottled plumage are that in pied birds there are some feathers that are entirely white, and the black markings are much more irregular than in mottled birds.

Down Color. The down color of pied chicks is practically the same as the down color of Mottled Ancona chicks.

Pied Plumage Recessive to Self-Black. In studies on the inheritance of pied plumage, Punnett and Pease (1927) came to the conclusion that pied plumage behaves as a simple recessive to full color. They found that a pied bird looks lighter when the pied character is associated with the Plymouth Rock type of barring "than when the same grade of piedness is on a self-black basis."

Since pied plumage is characteristic of the Exchequer Leghorn, further experiments were conducted by crossing a Black Leghorn male with Exchequer Leghorn females. It was found that the pied character behaves in the same way as the mottling character toward

black, each being recessive to black on a monohybrid basis, although the genetic relationship between piedness and mottling apparently has not been worked out.

THE INHERITANCE OF SPANGLING

The spangled character of plumage coloration, found in Silver-Spangled and Golden-Spangled Hamburgs, consists of a V-shaped black spangle at the tip of each feather, the rest of the feather except for the fluff at the base being white in the silver variety and gold in the golden variety.

Down Color. According to Dunn and Landauer (1930), the down color of Silver-Spangled Hamburg chicks is "a light bluish black indistinctly striped on the back with black and white. The tips of the dark down are yellowish white, giving the chicks a general silvered or dusty appearance. On the head and neck the base of the down is bluish black while the tips are yellowish white." According to Punnett (1923), the down color of Golden-Spangled Hamburg chicks is "chocolate brown with much wider stripes and a more or less golden head."

Acquiring the Spangled Pattern. Dunn and Landauer (1930) found that the pattern of the spangled fowl appears gradually during the growth of the chick through the replacement of the original non-spangled feathers by feathers showing the spangled pattern. They found that almost none of the feathers which developed before the chick was twenty-five days old showed the spangled pattern, whereas the feathers developing after that time showed it.

The Genetics of Spangling. The results secured by Lefevre (1917) and Lefevre and Rucker (1923) in crosses between Silver-Spangled Hamburgs and Brown Leghorns led them to conclude that spangling was dominant and sex-linked. The sex-linkage of spangling was not borne out, however, in results which Punnett (1923) secured from a cross of Silver-Spangled Hamburgs $\times$ Golden-Penciled Hamburgs since of 22 F_2 birds there were 16 spangled and 6 barred birds, 3 of the latter being males and 3 being females, whereas if spangling is sex-linked all the barred birds should have been females. Punnett says that spangling is probably related to lacing and barring but that the appearance of spangling depends upon a gene not found in laced and barred breeds.

The results secured by Taylor (1932) from reciprocal crosses between Silver-Spangled Hamburgs and Black Minorcas led him to conclude that spangling is due to a dominant autosomal gene, that is, spangling is not sex-linked. Taylor further observed that: "The

expression of spangling is partially or completely inhibited in the presence of extended black. A greater inhibition of spangling in female offspring than in male offspring may be due to the action of the female sex hormone on the development of black pigment in birds of genetically extended black types." Taylor found that birds homozygous for spangling were more completely spangled than birds heterozygous for spangling.

THE INHERITANCE OF THE "COLUMBIAN" PATTERN

There are five varieties having what is known as the "columbian" pattern of plumage: Columbian Leghorns, Columbian Plymouth Rocks, Columbian Wyandottes, Light Brahmas, and Light Sussex. The plumage in both sexes is white except that the neck feathers of the female, the hackle feathers of the male, and the wings and tail of both sexes contain black. The neck and hackle feathers, the tail coverts of the female, and the saddle and sickle coverts of the male are black laced with white. In addition, in the case of the Light Brahma the feathers on the shanks and toes are black laced with white.

Sturtevant (1912) and Dunn (1923*b*) observed that the columbian pattern of the Light Brahma and other columbian-colored varieties is due to the presence of the dominant sex-linked gene *S*, for "silver," and a nonsex-linked gene *e*, which restricts the black to the neck, wings, and tail. Light Brahma and similar males, being homozygous for silver, transmit it to their daughters and sons, whereas Light Brahma and other columbian-colored females, being heterozygous for silver, transmit it to their sons only. In addition, Dunn has suggested that there are multiple genes determining the amount of black pigment developed in the feathers of the neck, wings, and tail.

THE INHERITANCE OF LACING

Several breeds and varieties of fowl have feathers that are edged or bordered with a band of color differing from the ground color. The laced breeds and varieties include: Silver-Laced and Golden-Laced Wyandottes, White-Laced Red Cornish, Bearded and Nonbearded Silver Polish, Bearded and Nonbearded Golden Polish, and Silver and Golden Sebright Bantams. It is interesting to note that in the two laced varieties of Wyandottes the tails are black, whereas in the laced Polish varieties and in the Sebright Bantams the tail feathers are laced. There is probably a single gene difference between the black-laced white feather as found in the silver-laced varieties and the black-laced golden-bay feather as found in the golden-laced

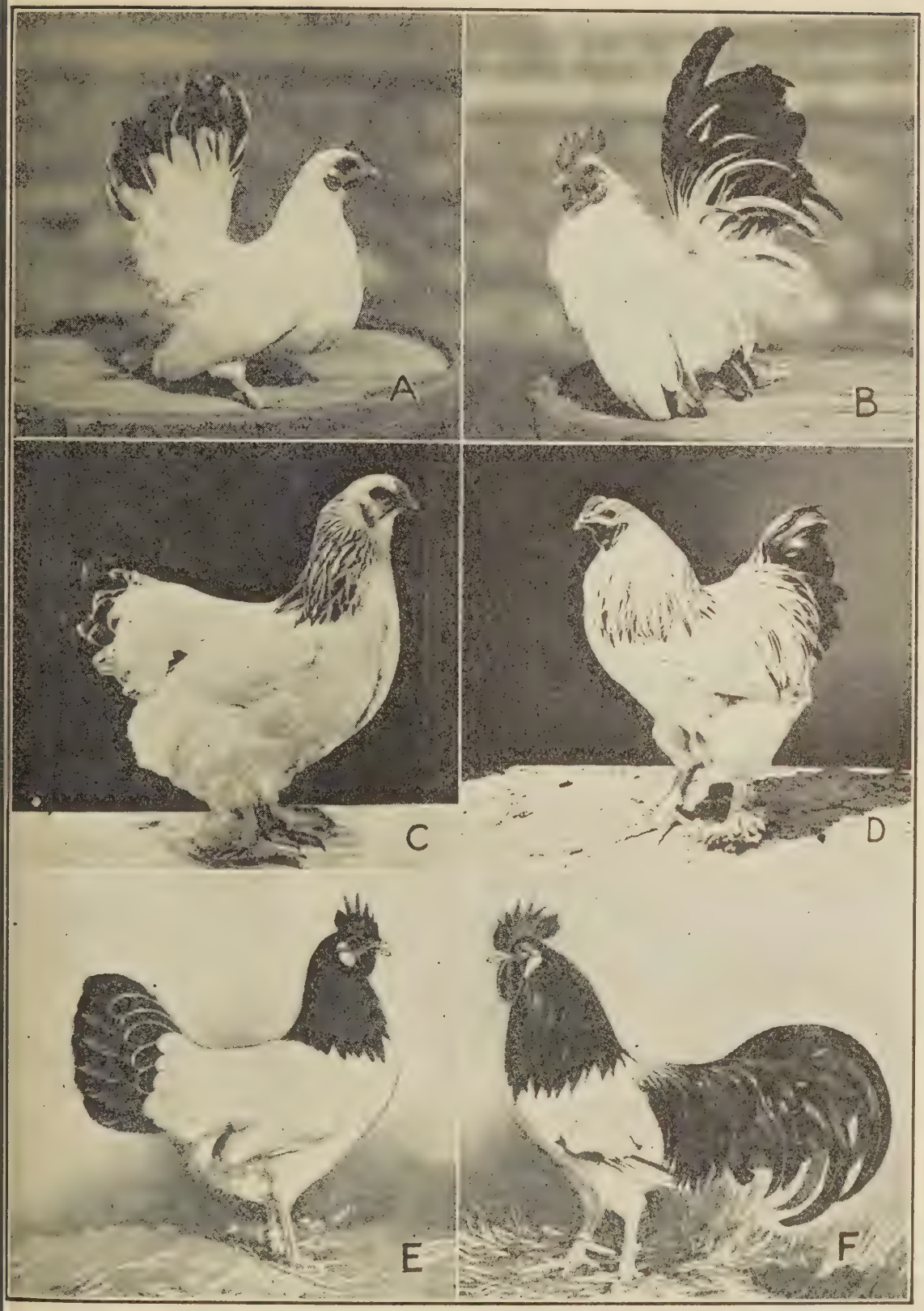

FIG. 31. Three varieties showing differences in the "extension" or the "restriction" of black. The Black-Tailed Japanese Bantams, shown in A and B, have black tails and black in some of the wing feathers, but there is no black in the neck and hackle feathers. The Light Brahmas, shown in C and D, with laced neck, hackle and saddle feathers, have what is called the "columbian" plumage pattern. The Lakenfelders, shown in E and F, have solid black necks, hackles, and tails and black in some of the wing feathers. (Photos by Reliable Poul. Jour.)

varieties. This matter is discussed later under the section on the inheritance of "silver" and "gold."

Punnett (1923) refers to a cross of the Silver Sebright Bantam × Golden-Penciled Hamburg, the F_1 results showing that the barring pattern of the Golden-Penciled Hamburg is dominant to the laced pattern of the Silver Sebright Bantam.

Agar (1924) crossed a Golden-Laced Wyandotte male × Barred Plymouth Rock females and then mated an F_1 male to a Golden-Laced Wyandotte female and was led to conclude that lacing is nearly completely epistatic to barring but is hypostatic to extended black. It is difficult to understand how lacing can be nearly completely epistatic to barring when it is well known that barring is dominant to extended black (nonbarring) and also apparently dominant to lacing, judging by the results which Punnett (1923) secured. It is quite obvious that much work remains to be done to establish the genetics of lacing upon a definite basis.

THE INHERITANCE OF PENCILING

In penciled plumage each feather has one or more stripes of the same shape as the outline of the feather but differing in color from the rest of the feather. The feathers of the female of the Dark Cornish have one stripe; those of the females of the Silver-Penciled Plymouth Rocks, Silver-Penciled Wyandottes, Dark Brahmas, Partridge Plymouth Rocks, Partridge Wyandottes, and Partridge Cochins have three stripes. The tail feathers of penciled females are black. None of the feathers of the males of any of the penciled varieties is penciled, as shown in Fig. 1. The difference between the silver-penciled and the partridge females is that in the silver-penciled varieties the black penciling is on a white background whereas in the partridge varieties the black penciling is on a reddish-bay ground color.

Up to the present, practically nothing is known concerning the genetics of penciling.

THE INHERITANCE OF BARRING

The inheritance of barring as a sex-linked character in Barred Plymouth Rocks has already been discussed in Chapter III. It was pointed out that the gene *B*, which produces the barring effect on each feather, is contained in the sex chromosome; the barred female being heterozygous for sex transmits the *B* gene to her sons only. The barred male being homozygous for sex transmits the *B* gene to his daughters as well as to his sons.

The barred breeds and varieties include the Barred Plymouth Rock, Dominique, Scotch Gray, Cuckoo Leghorn, Campine, and Golden-Penciled and Silver-Penciled Hamburg. In spite of the name, the two varieties of Penciled Hamburgs have barred feathers, although barring in the Campine and Hamburg behaves differently in inherit-

FIG. 32. When Rhode Island Red males are crossed with Barred Plymouth Rock females, the sex of the chicks can be distinguished at hatching time, as shown in this illustration. The females, solid black in down color, are shown on the left and the males, each with a light patch on the head, are shown on the right. As adults the females are black, sometimes with a tinge of red on the neck and breast, whereas the males are barred. The females have black or very dark shanks and toes, whereas the males have yellow shanks and toes. (U. S. D. A.)

ance from the barring in the Barred Plymouth Rock, Dominique, Scotch Gray, and Cuckoo Leghorn.

Down Color. The down color of the Barred Plymouth Rock chicks is black over the dorsal surface and on the sides except that there is a light yellowish-gray patch at the back of the head and the ventral surface is creamy white, the extent of which varies considerably. Punnett (1923) says, "In various experiments made at Cambridge it has been found that the light head patch invariably accompanies the barred plumage." In matings involving a cross between a Barred Plymouth Rock female and a male of a nonbarred variety, except the White Leghorns, the sex of the chicks can be distinguished at hatching time by the presence or absence of the light patch at the

back of the head. The chicks with the light head patch are males and those without it are females.

Quinn and Knox (1939) demonstrated that Barred Plymouth Rock chicks could be selected by sex based on down and shank color with a fair degree of accuracy. Male chicks had relatively large diffused silvery-white head spots, silvery white in the face and throat, silvery gray over the abdomen, and yellow or dusky yellow shanks and toes. Female chicks had relatively small white head spots, black in face with white spots, dark ashy gray or black with white spots over the abdomen, black or dark shanks, and black or dark toes with yellow in the extremities. Jerome (1939) was able to sex production-bred chicks with a relatively high degree of accuracy by the differences between the sexes in head spots and shank coloring. One of the chief differences noted with respect to head spotting was that the head spot in females was usually more regular in outline and was pointed anteriorly.

The down-color sexing of chicks secured from a mating of a Barred Plymouth Rock male $\times$ Rhode Island Red females was accomplished with an accuracy of about 65 per cent by Quinn and Knox (1939). About 91 per cent of the chicks with brown heads were males and about 79 per cent of the silver-striped chicks were females.

Lamoreux (1939) crossed a Barred Plymouth Rock male with Mottled Ancona females and from the F_2 generation selected chicks homozygous for mottling and homozygous or heterozygous for barring, both mottling and barring having a restricting effect on the complete extension of black pigment. Nearly all the F_2 chicks bearing a black head spot and black down over the back are females. Chicks lacking a head spot are males and nearly all those bearing a head spot and dilute black down over the back are males.

Although the down color of the Silver Campine chick is grayish brown and that of the Golden Campine chick is of a medium brown shade, it is sometimes difficult to distinguish the chicks of the two varieties because the median dorsal and the two lateral stripes along each side of the back are of such a rich dark chocolate color and are sometimes so wide as to obscure the ground color.

In the Golden-Penciled Hamburg the down color is of the striped form, the ground color being golden buff with striping along the median line of the head and back.

Barring Versus Nonbarring. The fact that barring is sex-linked was apparently first observed by Cushman (1893), although Punnett and Bateson (1903) and Spillman (1908) were the first to suggest that the inheritance of barring rested on a sex-linked basis, and

Morgan (1910) was apparently the first to explain that sex-linked characters were such as a result of the genes producing the characters residing in the sex chromosomes.

The inheritance of barring as a sex-linked dominant character has been demonstrated by a number of investigators, including: Goodale (1909, 1910), Pearl and Surface (1910*a*, 1910*b*), Morgan and Goodale (1912), Holdefleisz (1911), Frateur (1914), Dunn (1923), Jull (1924), and Punnett (1929).

Punnett and Pease (1930) have developed a breed called the Cambar out of matings between Barred Plymouth Rocks and Gold Campines, the Cambar having the unique distinction of producing within the breed chicks the sex of which can be distinguished at hatching time, when the male chicks have pale "blotchy" down color whereas the females have down color characteristic of the Gold Campine chicks.

Punnett and Pease (1939) have developed another autosex-linked breed in which the sex of the chicks can be distinguished at hatching time by the color of the down. The Legbar was developed from an original cross between a Brown Leghorn male mated to a Barred Plymouth Rock female. An F_1 male was mated to a Brown Leghorn female, and, among the progeny produced, there were "brown-barred" birds that were developed by selection into the breed known as the Legbar. These birds are of the Brown Leghorn type and plumage pattern except that they are barred and the sex of the chicks can be distinguished at hatching time.

Jaap (1940) has developed at the Oklahoma Experiment Station an autosexing variety called the "Oklabar" from an original mating of White Plymouth Rocks and Rhode Island Reds.

Table 10 gives the matings between nonbarred males and barred females that may be used to produce chicks whose sex can be determined at hatching time.

The Effect of the Sex-Linked Gene for Barring. Although it has been observed that barring is dominant to color and that the gene for barring is sex-linked, at the same time, Punnett (1923) points out that the barring in Barred Plymouth Rocks, Dominiques, Scotch Grays, and Cuckoo Leghorns is genetically quite distinct from the barring in Campines and Penciled Hamburgs, concerning the inheritance of which but little is known at present.

The gene for barring as found in Barred Plymouth Rocks is regarded as restricting the black pigment to bars, for if Barred Plymouth Rocks did not have the gene *B* they would be black. Dunn (1923*a*) states that the barring effect in Barred Plymouth Rocks, consisting as it does of alternate white and black bars, is dependent

TABLE 10. MATINGS INVOLVING THE SEX-LINKAGE OF BARRING WHICH MAKES IT POSSIBLE TO DISTINGUISH THE SEX OF CHICKS AT HATCHING TIME

Mating No.	Nonbarred Males	Barred Females	Color of Chick	Color of Adult Progeny
1	All black breeds and varieties.[1]	Barred Plymouth Rocks. Dominiques. Scotch Grays. Cuckoo Leghorns.	Males black on top of body except white spot on top of head. Beak, shanks and toes yellow. Females all black on top of body. Beak, shanks, and toes black or very dark.	Males barred. Beak, shanks, and toes yellow. Females black. Beak, shanks, and toes black or very dark.
2	Rhode Island Red, Buff Plymouth Rock and all other color varieties except blues.	Same as above.	Males and females same as in mating No. 1.	Males same as in mating No. 1 Females black except they may have some red or other color in the neck or over other parts of body. Beak, shanks, and toes black or very dark.
3	White Minorca and other white recessives except White Plymouth Rock.[2]	Same as above.	Males and females same as in mating No. 1.	Males and females same as in mating No. 1.
4	Cambar.	Cambar.	Males pale "blotchy." Females like Campines.	Males much paler in color than females

[1] Punnett (1929) points out that difficulty may be encountered in distinguishing the sexes of chicks at hatching time if Black Sumatra and Black Leghorn males are used, owing to the fact that the white normally present on the ventral surface of all chicks of black breeds and varieties may in the case of Black Sumatra male × barred female and Black Leghorn × barred female matings extend to the dorsal surface over the head and neck so that the sexes cannot be distinguished accurately.

[2] A White Leghorn or a La Bresse male could not be used in mating No. 3 because in each case the white is dominant to color and all the chicks would be white with a few black spots. The White Plymouth Rock male could not be used because, although it is a recessive white it carries the gene for barring, or at least most White Plymouth Rocks do, but all White Plymouth Rocks lack the gene for color.

upon two sex-linked genes, one of which is *B* for barring pattern and the other a gene which prevents the development of buff in what would otherwise be the white bars of the barring pattern. When this second gene, known as "silver," is absent, the barring pattern consists of black and "gold" bars instead of black and white bars. Punnett (1923) also observed that the Barred Plymouth Rock carries the gene for silver. As far as the inheritance of barring is concerned, however, the presence of the gene for the production of silver does not affect the situation.

Punnett and Pease (1928) have described a barred variety developed recently in England, the Gold-Barred Plymouth Rock, in which the black of the Barred Plymouth Rock is replaced by a rich buff, so that the Gold-Barred Plymouth Rock is barred with buff on a white background. The barring was found to be sex-linked as in the case of the Barred Plymouth Rock, and Punnett and Pease, in view of the results secured from various matings, have suggested that the genes for barring in the Barred variety and in the Gold-Barred variety differ in their inhibitory potency and are allelomorphic to one another. The gene *B* occurring in the Barred variety is regarded as being more potent than the gene *B'* occurring in the Gold-Barred variety. The latter variety is essentially a buff with the addition of the barring character.

Montalenti (1934) has suggested that the gene for barring exhibits a rhythmic activity in relation to hormone secretions and that width of barring is due to a gradient of hormone threshold.

It has been observed by Serebrovsky (1926), Kuhn (1928), Hertwig and Rittershaus (1929), and Juhn (1933) that, when Barred Plymouth Rocks are crossed with other breeds, there usually appear in the F_1 generation birds with red feathers or with feathers bordered with red. Juhn ascribes the appearance of these exceptional feathers to a reaction between the gene for barring and the influence of hormones affecting the rate of growth.

Hadley (1914) found that the gene for barring is present in both White Leghorns and White Plymouth Rocks, males being homozygous for this sex-linked gene (*BB*) and females being heterozygous (*B*—). The White Leghorn is white, however, because of the presence of the inhibiting gene *I*, and the White Plymouth Rock is white because of the absence of chromogen material. When the White Leghorn is crossed with a colored variety, the F_2 generation frequently contains some barred birds.

Punnett (1923) makes an interesting observation concerning the effect that the gene *B* in White Leghorns has on the color of hybrids

produced from matings of White Leghorns with colored varieties. He points out that, although the gene *I* exercises a more or less complete effect in inhibiting the development of pigmentation, the effect is augmented by the presence of the barring gene, *B*.

Barring in Campines Not Sex-Linked. In Barred Plymouth Rocks, Dominiques, Scotch Grays, and Cuckoo Leghorns the barring character is produced by alternating black and white bars. Among the Campines an interesting situation exists regarding three different kinds of barring. The Silver variety has black and white bars, the Golden variety black and golden-bay bars, and the Chamois variety white and golden-bay bars.

Since the plumage of the Silver is dominant to that of the Golden variety, Punnett (1923) points out that the white bars of the Silver variety are due to the action of a gene which inhibits the development of golden bay. This inhibiting gene is the same as the one that produces the difference between the silver and gold characters as explained a little later in this chapter. Punnett further points out that the plumage of the Chamois is dominant to the plumage of the Golden variety, the difference between white and golden-bay bars and black and golden-bay bars being due to a single gene, as Punnett and Pease (1921) have shown.

It is apparent, then, that the golden-bay bars of the Chamois variety correspond to the golden-bay bars of the Golden variety, and that the Chamois variety contains a gene which inhibits the development of the melanic pigment contained in the black bars of the Golden variety. Therefore, a cross between the Silver and Chamois varieties should produce white birds, which Punnett found to be the case.

By the use of appropriate symbols the production of white birds from a cross between the Silver and Chamois varieties is readily demonstrated. The Silver variety contains the gene *S* which inhibits the development of golden bay. The Golden and the Chamois varieties, therefore, carry *s*. The Chamois variety contains the gene I^b which inhibits the development of black. The Silver and the Golden varieties, therefore, carry i^b. The Silver variety is SSi^bi^b; the Golden variety is ssi^bi^b; the Chamois variety is ssI^bI^b. When the Silver and Chamois varieties are crossed the following result is secured.

	Silver Campine × Chamois Campine
P_1 zygotes	SSi^bi^b × ssI^bI^b
P_1 gametes	Si^b × sI^b
F_1 zygotes	SsI^bi^b

The F_1 zygotes SsI^bi^b develop into white birds because the gene S inhibits the development of golden bay and the gene I^b inhibits the development of black.

THE INHERITANCE OF "SILVER" PLUMAGE

The terms "silver" and "gold" are used with reference to two well-known ground colors of the down of chicks of several different breeds and varieties.

To the "silver" class belong the Silver-Laced and Silver-Penciled Wyandottes, Silver Campines, Silver-Penciled Plymouth Rocks, Silver-Spangled Hamburgs, Silver-Gray Dorkings, and other varieties, including those in which the ground color of the down is creamy silver, such as Salmon Faverolles, Light Brahmas, Light Sussex, Columbian Plymouth Rocks, and Columbian Wyandottes.

Davenport (1912) observed that in a cross between the Dark Brahma and the Brown Leghorn the "silver" character in the Dark Brahma was transmitted as a sex-linked character. That the Barred Plymouth Rock carries silver as well as barring has been demonstrated by Dunn (1923*a*, 1924) and Punnett (1923). Asmundson and Milne (1930) demonstrated that the Mottled Ancona carries silver. In a cross between White Leghorns and Brown Leghorns Punnett (1923) obtained some silver-grays in the F_2 generation, demonstrating that the White Leghorn carries the gene for silver.

The White Wyandotte, although it is a recessive white, has usually been found to possess the gene for silver, the White variety apparently having originated from the Silver-Laced variety as a sport. Warren (1930*b*) points out that difficulty arises, however, from the fact that the white plumage makes it impossible to detect individuals that do not possess the gene for silver and that some White Wyandottes also carry black and produce black chicks when crossed with gold varieties, it being impossible to determine the sex of the black chicks from their appearance.

To the "gold" class belong all breeds in which the ground color of the down is some shade of buff or golden brown, such as Buff Cochins, Buff Leghorns, Buff Orpingtons, Buff Plymouth Rocks, Buff Wyandottes, Rhode Island Reds, and Red Sussex. Also belonging to the gold class are those breeds or varieties in which the male is some form of black-red in plumage color, such as Barnevelders, Brown Leghorns, Cornish, Partridge Cochins, Plymouth Rocks and Wyandottes, and Golden-Laced Wyandottes.

The gene for silver is sex-linked, as demonstrated in the cross between Silver-Penciled and Partridge Plymouth Rocks made by

FIG. 33. A Silver-Penciled Plymouth Rock ♂ × Partridge Plymouth Rock ♀ produce F_1 silver males and females. An F_1 ♂ × F_1 ♀ produce an F_2 generation in which the males are silver and one-half of the females are silver but the other half are nonsilver. (Photo by U. S. D. A.)

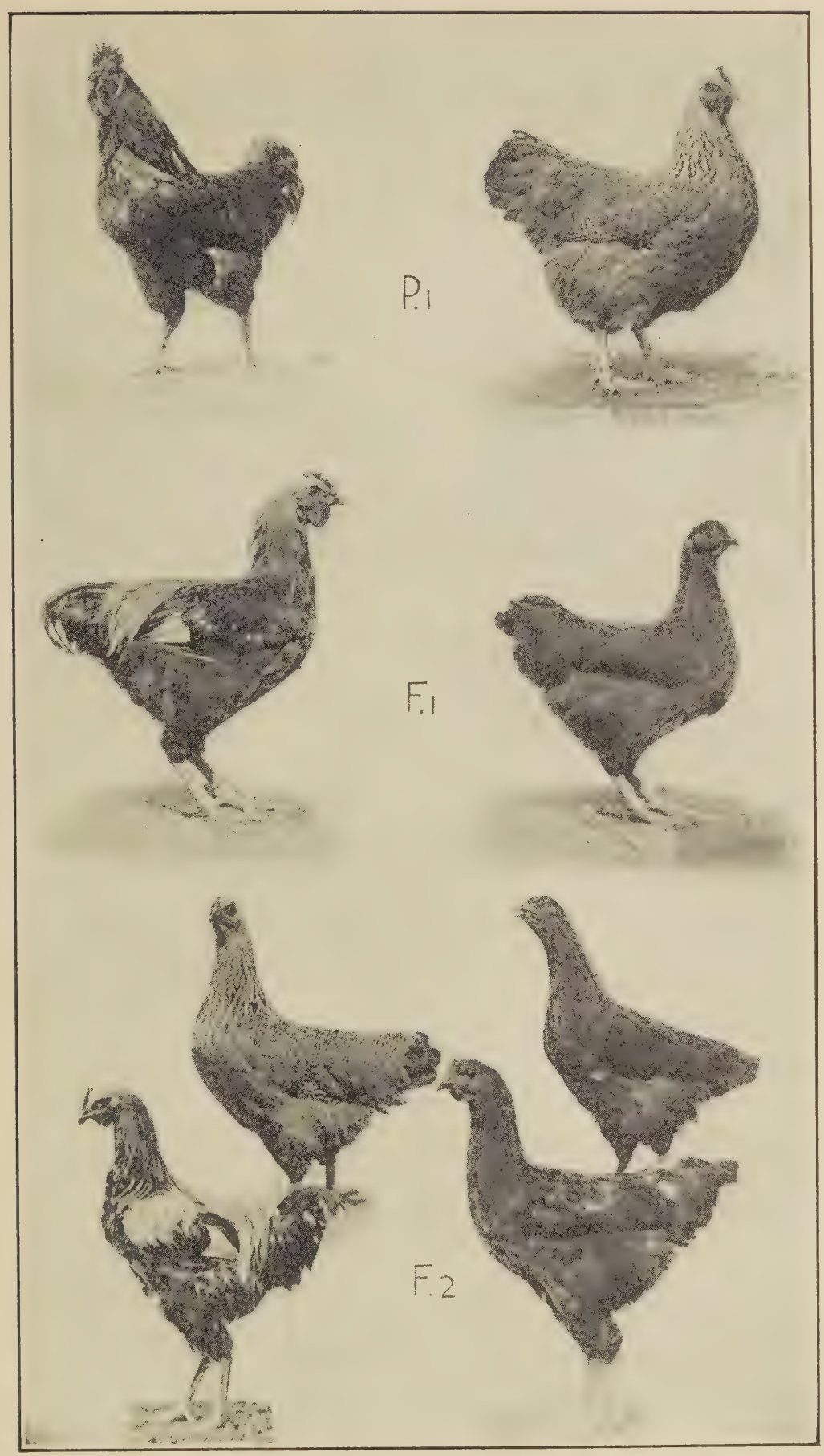

FIG. 34. A Partridge Plymouth Rock ♂ × Silver-Penciled Plymouth Rock ♀ produce F_1 silver males but nonsilver females, the sex-linked gene for "silver" being transmitted from the dam to her sons only. An F_1 ♂ × F_1 ♀ produce an F_2 generation in which one-half of each sex is silver and one-half is nonsilver. In this sex-linked cross it is difficult to distinguish the sex of the chicks at hatching time. (Photo by U. S. D. A.)

Jull and Quinn (1931). In this cross both varieties have the triple-penciled pattern character, so that the only difference is that one variety has white and the other gold.

The results of the crosses are illustrated in Figs. 33 and 34, and show that silver is sex-linked, being transmitted from dam to sons only but from sire to both sons and daughters. The Silver-Penciled Plymouth Rock male, therefore, is *SS* and the female is *S*—, the dash (—) representing the absence of a sex chromosome.

On the other hand, apparently "gold" is not sex-linked. The results secured from various matings of black males with gold females, such as Buff Orpingtons and Brown Leghorns, show that the F_1 females may sometimes carry varying amounts of gold in their black plumage. These results indicate that gold is not sex-linked. Knox (1927) has shown that when White Plymouth Rock (recessive white) males were mated to Buff Orpington females, the F_1 females were predominantly buff. These results also indicate that gold is not sex-linked.

The allele of the sex-linked "silver" gene is nonsilver, just as the allele of the sex-linked barring gene is nonbarring.

Distinguishing the Sex at Hatching Time. It has been found that when females belonging to the silver class are mated to males of the gold class the sex of the chicks can be distinguished at hatching time, with the exception of a few particular crosses.

The following table, taken from Warren (1930*b*) with a few minor changes, shows the color of the chicks at hatching time and their color when they become adults in various matings between silver and gold breeds and varieties.

Warren (1930*b*) points out that the female chicks can be more easily distinguished from the male chicks at hatching time if the columbian pattern is involved in the mating. He also points out that if a Brown Leghorn male is mated to females of the silver-laced or silver-penciled varieties the chicks have such a broad dark stripe over the back that it is sometimes difficult to distinguish the sexes of the chicks. Jull and Quinn (1931) found that when a Partridge Plymouth Rock male is mated to Silver-Penciled Plymouth Rock females it is impossible to distinguish the sexes at hatching time with any degree of accuracy, although the difference between the F_1 silver and gold birds in the adult plumage is quite marked, as shown in Fig. 34.

Hormones for Testing Genotypes. When certain crosses are made, the F_1 results secured have seemed to indicate that sex-linked inheritance was involved, whereas when adequate tests have been applied such has been found not to be the case. This was found to

TABLE 11. MATINGS INVOLVING THE SEX-LINKAGE OF SILVER WHICH MAKES IT POSSIBLE TO DISTINGUISH THE SEX OF CHICKS AT HATCHING TIME

Mating No.	Gold Males	Silver Females	Color of Chick	Color of Adult Progeny
1	Rhode Island Red	White Wyandotte. Silver-Penciled Plymouth Rock. Silver-Penciled Wyandotte. Silver-Laced Wyandotte. Columbian Plymouth Rock. Columbian Wyandotte. Light Sussex. Dark Brahma. Light Brahma.	Males cream or white may show smokiness in down. Females buff or red color. Both sexes may show narrow striping.	Males columbian pattern. Females buff to red; may show some stippling or striping.
2	Buff varieties: Buff Leghorn. Buff Minorca. Buff Plymouth Rock. Buff Wyandotte. Buff Cochin.	Same as above.	Same as in mating No. 1 except female chicks generally lighter in color.	Same as in mating No. 1 except females usually buff.
3	Brown Leghorn. Partridge Plymouth Rock. Partridge Wyandotte. Golden-Laced Wyandotte.	Columbian Plymouth Rock. Columbian Wyandotte. Light Brahma. Light Sussex.	Same as in mating No. 1.	Same as in mating No. 1.

be true in the case of the inheritance of spangling, which has already been discussed.

In certain crosses, as for instance when Jull and Quinn (1929) crossed a Black Rose-Comb Bantam male with White Rose-Comb Bantam females and secured F_1 black females and F_1 black males except that they had red lacing in the hackle and in the saddle feathers

and red on the shoulders, it is sometimes assumed that the results secured are due to sex-linked inheritance. However, Caridroit and Regnier (1930), Taylor (1933), and Regnier (1933), and Quinn and Burrows (1935) have shown that such is not the case.

Quinn and Burrows (1935) crossed a Black Sumatra male with a White Wyandotte female and observed that the F_1 progeny at hatching time were all black but that at about four months of age the F_1 males began to show gold and silver in the hackle and saddle feathers, whereas the F_1 females were still black. This would seem to indicate sex-linked inheritance. The White Wyandotte female carried the sex-linked gene for silver, as had been previously demonstrated by the results secured from mating her with a Rhode Island Red male. An F_1 female from the mating of a Black Sumatra male and a White Wyandotte female would not receive the sex-linked silver gene from her dam, and ovariotomy of an F_1 black female resulted in her assuming male-type plumage with red in the wing bows and saddle, showing that she was a potential gold, *s—Ee,* and did not carry silver. The results also demonstrated that the Black Sumatra sire did not have the gene for silver. When an F_1 black male showing silver and gold lacing in the hackle and saddle was castrated and given injections of theelin (a female sex hormone), black feathers of the female type developed in the new feathers that replaced those plucked prior to the injections. The results secured demonstrate that the Black Sumatra male was nonsilver as far as his genotype was concerned and that the black plumage of the F_1 females was due to the elaboration of the female sex hormone by the ovary, the hormone having a melanizing effect on the plumage.

THE INHERITANCE OF EARLOBE COLOR

The color of the earlobe in the case of many breeds is a breed characteristic, by which is meant that all birds belonging to a certain breed must have the same color of earlobe. All Leghorns, regardless of variety, have white earlobes. Leghorns, Minorcas, and Anconas comprise most of the white-earlobe breeds, and Plymouth Rocks, Rhode Island Reds, Wyandottes, Orpingtons among many other breeds have red earlobes.

The inheritance of earlobe color has apparently received but little attention, since the only work that seems to have been done is that by Warren (1928). Crosses were made involving three varieties of Leghorns, the Single-Comb White, the Rose-Comb Brown, and the Single-Comb Buff, and the following varieties having red earlobes:

Barred Plymouth Rock, Dark Brahma, White Wyandotte and Silver-Laced Wyandotte, Single-Comb Rhode Island Red, as well as the Jersey Black Giant breed. Earlobe color in the progeny of various crosses was determined at six months of age since Warren found that prior to this a change in color sometimes took place.

Warren found the inheritance of earlobe color to be very complex, and briefly it may be said that his results indicate that earlobe color is dependent upon the action of several genes, neither white nor red being dominant.

THE INHERITANCE OF EYE COLOR

Punnett (1923) has suggested that a close relation existed between down color and the presence of pigment in the iris in F_1 and F_2 chicks produced from a cross between Golden-Penciled Hamburg males and Silver Sebright Bantam females. Punnett also points out that when a Brown Leghorn male is mated to Black Langshan females the F_1 birds of both sexes have red to orange-red in the iris, whereas when a Black Langshan male is mated to Brown Leghorn females the F_1 males have a red iris but the F_1 pullets have a black iris.

From observations on eye color in Rhode Island Reds, Warren (1929) noted that no relationship existed between chick down color and adult eye color. Warren and Gordon (1933), in studying eye-color inheritance in Rhode Island Reds, were not able to determine that variations in eye color are inherited, but there was no evidence of sex-linked genes being involved.

THE INHERITANCE OF SKIN COLOR

Many breeds of poultry have yellow skin, many others have white skin, and one breed, the White Silkie, has black or violet colored skin. Yellow-skinned breeds include the Leghorns, Plymouth Rocks, Wyandottes, Rhode Island Reds, and many others. White-skinned breeds include Langshans, Orpingtons, Minorcas, Sussex, Dorkings, and others. The inheritance of skin color has been investigated only recently and only by a few investigators.

Yellow Versus White Skin. The difference between yellow skin and white skin is due to the presence of lipochrome (animal fat) pigment in the former and its absence in the latter.

Punnett (1923) was apparently the first to report the dominance of white skin color to yellow skin color. Anderson and Martin (1924) crossed Buff Orpingtons and White Leghorns as well as White Minorcas and White Plymouth Rocks and observed white skin to be dominant

to yellow skin. Lambert and Knox (1927) confirmed this fact in reciprocal crosses between white-skinned and yellow-skinned breeds. The results secured indicate quite clearly that white skin is dominant to yellow skin on a monohybrid basis and that skin color is not sex-linked.

In crosses of a Mottled Ancona male × Black Orpington females and a Black Minorca male × Mottled Ancona females, Asmundson and Milne (1930) secured results that likewise show that white skin is dominant to yellow skin and that one pair of genes accounts for the difference. White-skinned breeds have the genetic constitution *WW* and yellow-skinned breeds *ww*.

Black Skin. Mention has been made of the fact that the skin of the White Silkie is black or violet colored, and in this respect the Silkie differs from all other breeds. Kuklenski (1916) has shown that the Silkie skin color is due to chromatophores distributed in varying density throughout the connective tissue, periost of the bones, and other organs. The epithelium, or outer layer of cells of an organ, is unpigmented, but the bird when plucked appears to be black because of the dark color of the underlying tissues.

In crosses between Silkies and Brown Leghorns, Bateson and Punnett (1911) explained their results by assuming that two genes are involved: (1) a dominant nonsex-linked gene for mesodermal pigment (*PP*), and (2) a dominant sex-linked inhibitor of mesodermal pigment (*DD*). On their hypothesis the Silkie male is *PPdd* and the Silkie female *PPd*—; the Brown Leghorn male is *ppDD* and the Brown Leghorn female *ppD*—.

Dunn and Jull (1927), from a cross between a White Silkie male and White Leghorn females, concluded that their data, although supporting the hypothesis of a sex-linked inhibitor of mesodermal pigment, indicate that the development of mesodermal pigment may be due to the effects of multiple genes or that in White Leghorns, in addition to *D* which inhibits the development of mesodermal pigment, the gene for barring apparently tends to modify the development of mesodermal pigment.

THE INHERITANCE OF SHANK COLOR

Since there are several shank colors among the breeds and varieties of the domestic fowl, as pointed out in Chapter I, it is natural to expect that the inheritance of shank color should prove to be a complicated problem.

Shank colors most frequently encountered include white, yellow,

black, blue, gray, willow, pinkish white, and pearl. These colors are the result of the presence or absence of one or more different kinds of pigments in either one or both of the two layers of the skin. The outer layer of the skin is the epidermis and the inner layer is the dermis. The outer layer of the epidermis is modified into scales, which vary in size and shape. According to Hanau (1881), the epidermis is invariably thinner than the dermis.

The various colors of the shank are due to the presence of two kinds of pigment, which Hanau (1881), Jeffries (1883), and Gadow (1891) have called orange-yellow and brownish-black. The orange-yellow is a lipochrome pigment made up of animal fat cells, the pigment in concentrated form giving an orange color and in more dilute form a yellow color. The so-called brownish-black is in reality a melanic pigment.

The most intensive histological study of shank colors in the domestic fowl is that of Barrows (1914), although the inheritance of shank color was not studied. Among the more important observations of Barrows are the following: (1) white shanks are the result of lack of pigment. (2) Yellow shanks and various shades of yellow are due to the presence of lipochrome pigment in the epidermis, melanic pigment being absent from the dermis. (3) Willow shanks and green shanks are due to the presence of lipochrome pigment in the epidermis and melanic pigment in the dermis. (4) Black shanks are the result of melanic pigment in the epidermis and in some cases also in the dermis; if lipochrome is present the bottoms of the feet are yellow and if lipochrome is absent the bottoms of the feet are white. (5) Blue shanks are the result of the presence of melanic pigment in the dermis when it is absent from the epidermis and lipochrome pigment is absent from both dermis and epidermis. (6) All shades, except red and pink, are the result of various combinations of lipochrome and melanic pigment in the epidermis and dermis.

Among the earliest observations concerning the specific nature of shank-color inheritance are those of Punnett (1925). In a cross of a Brown Leghorn male $\times$ Gold-Penciled Hamburg females the F_1 birds of both sexes had light-colored shanks, whereas in the reciprocal cross the F_1 males had light-colored shanks but the F_1 females had dark-colored shanks. These results demonstrate that the brown Leghorn female carries an inhibitor for the development of dark shanks in a heterozygous form, the inhibiting gene being sex-linked.

The fact that Black Leghorn females frequently have black spots in an otherwise yellow shank whereas Black Leghorn males are usu-

ally free of such spots is accounted for by the fact that the female has the sex-linked inhibiting gene in a heterozygous form and the males have it in a homozygous form.

The sex-linked nature of the gene *B*, for barring, which inhibits the development of dark shanks is clearly demonstrated in a cross made by Jull and Quinn (1931) between a Rhode Island Red male and Barred Plymouth Rock females in which the F_1 males had yellow shanks and the F_1 females had black or very dark-colored shanks. It is easy to understand from this why purebred Barred Plymouth Rock females frequently have dark spots on their shanks but males are nearly all free of such spots.

According to Punnett (1923), highly developed epidermal pigment in the shanks seems to be associated with some form of black or dark-brown plumage. Warren (1928*a*) has pointed out that the genes for certain plumage colors also appear to affect the color of the shanks. Asmundson and Milne (1930) report that in crosses between each of two black-shanked varieties, Black Minorca and Black Orpington, and a yellow-shanked breed, Mottled Ancona, the F_2 generation consisted of birds with solid black plumage that always had black, bluish-black or greenish-black shanks, and birds with mottled plumage that had white or yellow shanks spotted with black.

Genes for Shank Color. The inheritance of shank color has been most intensively studied by Dunn (1925). According to him there are two pairs of genes which tend to inhibit the development of pigment, one being sex-linked and the other not sex-linked. The gene *W* inhibits the development of lipochrome pigment in the epidermis and is present in birds with shanks that are white, pinkish white, pearl, blue, slate, or gray. *W* is practically completely dominant and is not sex-linked. The gene *D* tends to inhibit the development of melanic pigment in the dermis and is present in birds with shanks that are yellow, white, or pearl. *D* is nearly completely dominant and is sex-linked.

Knox (1935) made several crosses for the purpose of determining the nature of the inheritance of shank color, the results of which have shown that certain genes effect the distribution of melanic pigment in the shanks. Observations on the shank color of the F_1 progeny secured from reciprocal matings of Jersey Black Giants and Rhode Island Reds led Knox to conclude that one kind of dark shanks was autosomal and was due to the effects of the gene *E*, which caused the extension of melanic pigment in the shanks in much the same manner as in the plumage. The F_1 males showed less black in the plumage and

less melanic pigment in the shanks than the F_1 females, the difference being due apparently to the melanizing effects of the female sex hormones elaborated by the ovary.

The results of a mating of an F_1 male, the progeny of a cross of a Buff Orpington male × Barred Plymouth Rock females, mated to Rhode Island Red females, led Knox to conclude that the barring gene *B* restricts black in the plumage to produce barring but also restricts the deposition of melanic pigment in the shanks.

Knox made reciprocal matings between Jersey Black Giants and White Leghorns and also mated a Black Minorca male with White Leghorn females, from which it was concluded that the color-inhibiting gene *I* has a diluting effect on melanic pigment in the shanks. Knox also observed that the gene *c*, the allele of the chromogen gene *C*, has a similar diluting effect on melanic pigment in the shanks. Apparently all genes that restrict the extension of black in the plumage tend to restrict the extension of melanic pigment in the shanks.

Sturkie, Godbey, and Sherwood (1937) crossed Black Langshan males with White Leghorn, White Orpington, and Brown Leghorn females, respectively, and secured results similar to those secured by Knox (1935) and in addition postulated the existence of a sex-linked gene, which inhibits melanic pigment in the lower strata of the shanks. The allele of this sex-linked gene gives rise to blue or willow shank color, according to Sturkie, Godbey, and Sherwood.

From data available from various sources, Knox (1935) has submitted the following outline of the genes involved in shank color inheritance, all heterozygotes being omitted:

WW non-lipochrome (white color)
BB sex-linked barring plumage pattern restricts the black plumage to bars and practically a dominant restrictor of melanic pigment in the shanks.
[1]*DD* inhibitor of melanic (dark) shank color. Sex-linked.
EE extension of black plumage color, and of melanic pigment in the shanks.
CC chromogen for plumage color non-restrictor of melanic pigment in the shanks.
II inhibitor of plumage color, dilutes the melanic pigment in the shanks.

ww lipochrome (yellow color).
bb non-barred plumage pattern, no restriction of melanic pigment in the shanks.
dd sex-linked gene for melanic pigment in the shanks.
ee non-extension of black plumage and shank color.
cc lacks chromogen and has a diluting effect on the melanic pigment in the shanks.
ii non-inhibitor of plumage color and non-inhibitor of melanic pigment in the shanks.

The Effect of Varying Combinations of the Above Genes upon Shank Color[2]

Males	Females	
	1. Barring—Black Plumage Series	
WWDDBBEE	*WWD-B-EE*	white shanks (neither lipochrome nor melanic pigment present).
wwDDBBEE	*wwD-B-EE*	yellow shanks (lipochrome, melanic pigment, *EE*, and restrictor, *BB*, all present).
[3]*WWddBBEE*	*WWd-B-EE*	possibly blue shanks (no lipochrome present but melanic pigment, *EE* and *dd*, and restrictor, *BB*, present).
[3]*wwddBBEE*	*wwd-B-EE*	possibly dark or green shanks (lipochrome, melanic pigment, *EE* and *dd*, and restrictor, *BB*, present).
	2. Barring—Non-black Plumage Series	
WWDDBBee	*WWD-B-ee*	white shanks (neither lipochrome nor melanic pigment present).
wwDDBBee	*wwD-B-ee*	yellow shanks (lipochrome pigment present but no melanic pigment present).
[3]*WWddBBee*	*WWd-B-ee*	possibly blue or light blue shanks (no lipochrome but melanic pigment, *dd*, and restrictor, *BB*, present).
[3]*wwddBBee*	*wwd-B-ee*	possibly green or light green shanks (lipochrome, melanic pigment, *dd*, and restrictor, *BB*, all present).
	3. Non-barred—Black Plumage Series	
WWDDbbEE	*WWD-b-EE*	dark shanks (neither lipochrome nor restrictor, *BB*, present but melanic pigment, *EE*, present).
wwDDbbEE	*wwD-b-EE*	dark shanks (lipochrome and melanic pigment, *EE*, present but restrictor, *BB*, absent).
[3]*WWddbbEE*	*WWd-b-EE*	dark shanks (neither lipochrome nor restrictor, *BB*, present but melanic pigment, *EE* and *dd*, present).
[3]*wwddbbEE*	*wwd-b-EE*	dark shanks (lipochrome and melanic pigment, *EE* and *dd*, present and restrictor, *BB*, absent).
	4. Non-barred—Non-black Series	
WWDDbbee	*WWD-b-ee*	white shanks (no lipochrome, melanin, or restrictor present).
wwDDbbee	*wwD-b-ee*	yellow shanks (lipochrome present; melanic pigment and restrictor absent).

WWddbbee	*WWd-b-ee*	dark shanks (blue) (melanic pigment, *dd*, present; lipochrome and restrictor absent).
wwddbbee	*wwd-b-ee*	dark shanks (green) (lipochrome and melanic pigment, *dd*, present; restrictor absent).

5. Chromogen Series

A. Non-barred black

WWDDbbEECC	*WWD-b-EECC*	dark shanks (lacks lipochrome; melanic pigment, *EE*, and chromogen present).
wwDDbbEECC	*wwD-b-EECC*	dark shanks (lipochrome, melanic pigment, *EE*, and chromogen present).
WWDDbbEEcc	*WWD-b-EEcc*	blue or slaty blue shanks (lipochrome, restrictor, and chromogen absent; melanic pigment, *EE*, present).
wwDDbbEEcc	*wwD-b-EEcc*	green shanks (chromogen and restrictor absent; melanic pigment, *EE*, and lipochrome present).

B. Barred—Black

[3]*WWDDBBEECC*	*WWD-B-EECC*	white shanks (lacks lipochrome; melanic pigment, *EE*, restrictor, *BB*, and chromogen, *CC*, present).
wwDDBBEECC	*wwD-B-EECC*	yellow shanks (lipochrome, melanic pigment, *EE*, chromogen, *CC*, and restrictor, *BB*, all present).
[3]*WWDDBBEEcc*	*WWD-B-EEcc*	white shanks (as above, except chromogen genes lacking).
wwDDBBEEcc	*wwD-B-EEcc*	yellow shanks (as above, except chromogen genes lacking).

6. Inhibitor of Plumage Color Series

[3]*WWDDBBEEII*	*WWD-B-EEII*	white shanks (lacks lipochrome,with melanic pigment, *EE*, restrictor, *BB*, and inhibitor of plumage pigments *II* present).
wwDDBBEEII	*wwD-B-EEII*	yellow shanks (lipochrome, melanic pigment, *EE*, restrictor, *BB*, and inhibitor of plumage pigments, *II*, all present).
[3]*WWDDbbEEII*	*WWD-b-EEII*	blue shanks (lacks lipochrome and restrictor, *BB*, with melanic pigment *EE*, and inhibitor, *II*, present).
wwDDbbEEII	*wwD-b-EEII*	dark green shanks (restrictor, *BB*, absent; with lipochrome, melanic pigment, *EE*, and inhibitor of plumage pigments present).

[1] At present not critically differentiated from the barring genes, *BB*.

[2] All heterozygotes omitted.

[3] Genotypes at present not demonstrated.

Whether the genotypes given above cover all cases remains to be determined, since Punnett (1923) has suggested that there are indications that the presence of dermal pigment in certain instances is dominant to its absence.

Table 12. Dominant and Recessive Color Characters in Chickens

Character	Dominant or Recessive	Autosomal or Sex-Linked
White plumage	In White Leghorns, almost completely dominant to color	Autosomal
White plumage	In White Dorkings, Langshans, Minorcas, Plymouth Rocks, Wyandottes, recessive to color	Autosomal
White plumage	In some strains of White Rose-Comb Bantams and White Silkies, recessive to color	Autosomal
Red-splashed white plumage	Recessive to solid color and to color pattern	Autosomal
Albino	Recessive to normal	Autosomal
Black plumage	Dominant to recessive white	Autosomal
Blue plumage	Due to heterozygous condition of color genes	Autosomal
Red plumage	Recessive to black	Autosomal
Buff plumage	A multiple-gene character dominant to recessive white and recessive to black	Autosomal
Silver plumage	"Silver" in columbian, silver-laced and silver-penciled varieties dominant to nonsilver in red, buff, golden-laced and golden-penciled varieties	Sex-linked
Barred plumage	In Plymouth Rocks, dominant to nonbarring	Sex-linked
Barred plumage	In Campines, dominant to nonbarring	Autosomal
White skin and shank color	Dominant to yellow skin and shank color	Autosomal
Dark skin and shank color	Recessive to nondark skin and shank color	Sex-linked

Gynandromorphism and Lateral Asymmetry. So far in this chapter, the discussion has had to do with the normal inheritance of color characters, but occasionally a bird is observed that is abnormal because it possesses two or more colors that are normally allelomorphic to each other. Most of these cases have proved difficult to account for, but are important from the standpoint of the challenge they present to existing knowledge of the fundamental principles of inheritance.

Some of the simplest color aberrations that have been reported are those individuals with one shank of one color and the other shank of another color. Knox (1931) has reported the following cases: (1) An F_1 bird secured from a cross between a Black Langshan and a White Plymouth Rock had white shanks, one of which, however,

had a distinct yellow streak; (2) an F_1 female secured from a cross between a Rhode Island Red male and a White Wyandotte female had a green and a yellow shank. Knox suggests that probably a mutation occurred in one of the genes that is responsible for melanic pigment, thus giving rise to a yellow shank in a bird that would normally have had green shanks, a character fairly common among purebred White Wyandottes. A similar case has been observed by Crew (1932) except that the right shank was white and the left shank yellow.

Two interesting cases of color mosaics, similar in nature, have been reported by Lambert (1929) and by Knox (1931). The first case was that of an adult hen, killed and plucked before the asymmetry of skin color was discovered, the left half of the body being white-skinned and the right half, yellow-skinned. No details are given concerning the second case. Lambert pointed out that his case might be accounted for through the occurrence of a gene mutation but was more likely due to somatic nondisjunction of the chromosomes carrying the genes for skin color, assuming that the bird was heterozygous for skin color. In discussing this case, Hutt (1929) pointed out that if it were a case of nondisjunction, the chromosome carrying the gene for skin color would also carry genes for other characters, such as those for size, so that the two halves of the body would show other dissimilarities, which, however, were not apparent. Hutt suggested that the phenomenon could be more logically accounted for on the basis of a mutation in the skin-color gene. Hutt assumed that the bird was a Leghorn homozygous for yellow skin and that a dominant mutation occurred from *ww* to *Ww*, although, as both Hutt and Lambert noted, the bird might have been heterozygous for skin color, in which case, a recessive mutation occurred in the *W* gene.

Three cases of color mosaics involving also lateral asymmetry of skeletal development have been reported by Macklin (1923), Crew (1928), and Roberts and Quisenberry (1935), respectively. Macklin's specimen was one which exhibited not only gynandromorphism in plumage but also differences in size between the bones of the right and left limbs, and on the right side of the bird there was testicular tissue and on the left side ovarian tissue. Apparently, the loss of the sex chromosome from one side resulted in the loss of certain genes for size which differentiate males from females in skeletal dimensions.

Crew's specimen was a male from a cross between a Rhode Island Red male mated to a Light Sussex female. This bird was heterozygous for white and yellow skin color and had larger bones on the white-skinned side than on the yellow-skinned side. The lateral

asymmetry of skin color and skeleton was attributed by Crew to nondisjunction of the chromosomes carrying the genes for these characters.

The specimen of Roberts and Quisenberry had on the right side the general appearance of a Barred Plymouth Rock, with barred plumage and a nonfeathered shank, and on the left side, the general appearance of a Light Brahma, with columbian plumage pattern and a feathered shank; also, the limbs of the right side were shorter than the limbs of the left side. The breeder from whom this interesting specimen was secured had nothing on his premises but Barred Plymouth Rock females and Barred Plymouth Rock and Light Brahma males.

On the assumption that the gene *E* for the extension of melanic pigment and the gene *F* for feathering on the shanks are located on the same chromosome and are linked, Munro (1938) has suggested that the Roberts and Quisenberry specimen may be accounted for on the basis of the nondisjunction of a single autosome. Munro assumed that the egg of the Barred Plymouth Rock female had been fertilized by a spermatozoon from a Light Brahma male so that the specimen under consideration would be heterozygous for *F* and *E* and would be, therefore, an *FfEe* individual. If *F* and *E* are located on the same chromosome, *F* and *e* would enter the zygote on the Light Brahma chromosome, whereas *f* and *E* would enter the zygote on the Barred Plymouth Rock chromosome. Munro maintained that, if at the first division of the chromosomes the *Fe* genes failed to separate, or if after separation they failed to migrate to the proper reproductive cell, the cell giving rise to the gynandromorphic specimen would contain two Brahma-derived chromosomes, each carrying genes *F* and *e* and one Barred Plymouth Rock chromosome carrying *f* and *E*. If such took place, Munro maintained that the left side of the Roberts and Quisenberry specimen would be *FFfeeE* and the right side *fE*. According to Munro's theory of gene balance, when two *e*'s are present within the same cell, it is quite possible that their effects exceed those produced by only one *e*, in which case the feathers would lack pigment except in the hackle, wing, and tail and would resemble the Light Brahma. It follows, therefore, that a bird which is *FFfeeE* on the left side and *fE* on the right side would resemble the specimen reported by Roberts and Quisenberry.

Crew and Munro (1938), in a general review of practically all known cases of color mosaics, gynandromorphism, and lateral asymmetry in birds, mention several cases that have not been discussed so far.

The first case was an Old English Game bantam hen whose plumage on the left side was partridge colored with a white tip at the end of each feather and whose plumage on the right side was spangled with a black tip at the end of each white feather.

The second case was a Light Sussex cockerel whose right side was white-skinned and whose left side was yellow-skinned, with the bones on the right side slightly larger than those on the left.

The third case was a female secured from a mating of a Rhode Island Red male and a Light Sussex female. The right side, including the shank, was white except that the head and beak were yellow. The left side, including the shank, was yellow. The right shank had a male-like spur and the right side was about 13 per cent larger than the left side. When the bird was six years old, it was killed and upon examination, it was found to have a testis-like organ in complete spermatogenesis on the right side and an ovary on the left side. It is apparent that male-type skeletal structure, including a spur and testicular tissue, can persist in tissue which possesses the typical female sex-chromosome constitution.

The fourth case was a Rhode Island Red that had the following characteristics: female feathering except for a few saddle feathers; both shanks yellow, but the left one paler; the right side about 11 per cent larger than the left side; a testis containing mature spermatozoa on the right side; an ovary and an oviduct on the left side.

Crew and Munro (1938) also discussed the case reported by Veechi (1936) and the case reported by Hutt (1937). Veechi's bird possessed the following characteristics: a large male-like comb; mottled white and brown-black plumage on the left side; brown-black with practically no white on the right side; a male-type spur on each shank; the right side was about 13 per cent larger than the left side—the larger right side had the dominant naked-neck character (the inheritance of which is discussed in the next chapter) the left side had normal male-type hackle feathers, the rest of the plumage being female type; the right side had a normal testis; the left side had an ovotestis, but there was no oviduct.

Hutt's bird was originally sold as a pullet, but later crowed and behaved as a male and still later behaved more like a female. The plumage and shank color on the right side was lighter than on the left side. Except for many saddle feathers on the right side, the plumage was of the female type. The right side was approximately 15 per cent larger than the left side. The right side had a testis and normal vas deferens and motile spermatozoa were produced, although when females were artificially inseminated their eggs were infertile. The

left side of the bird had an ovary and an oviduct. Hutt suggested that this gynandromorph was produced as the result of the loss of a sex chromosome in a zygote originally male.

Crew and Munro (1938) have suggested that in those cases in which there were no reported differences or very slight differences in the size of the right and left sides, the aberration in plumage color is due to the elimination of an autosome from one of the two daughter cells that result from the first cleavage division. In those cases in which there was a lateral size difference amounting to about 10 to 15 per cent, it has been suggested that the cause is due to nondisjunction, one of the two daughter cells resulting from the first cleavage division being haploid in respect of a particular chromosome, the other daughter cell being triploid, similar to the situation in the Roberts and Quisenberry bird as reported by Munro (1938).

PROBLEMS

1. Give the genotypes and phenotypes for plumage color that are produced in the F_1 and F_2 generations in the following crosses:

White Leghorn male × White Minorca female.
White Wyandotte male × White Rose-Comb Bantam female.
White Silkie male × White Plymouth Rock female.
White Minorca male × White Silkie female.

2. What set of conditions give rise to the development of color in birds?

3. From the standpoint of barring only, give the results expected in the F_1 and F_2 generations in the following crosses:

Barred Plymouth Rock male × Black Hamburg female.
Black Hamburg male × Barred Plymouth Rock female.
Silver Çampine male × Black Hamburg Female.
Black Hamburg male × Silver Campine female.
Silver-Penciled Hamburg male × Black Hamburg female.
Black Hamburg male × Silver-Penciled Hamburg female.
Black Hamburg male × White Plymouth Rock female.

4. In testing for evidence of sex linkage what backcross mating should be made?

5. What are the F_1 birds like in the following crosses:

Blue Andalusian male × Black Orpington female.
Blue Orpington male × White Leghorn female.
Blue Andalusian male × Blue Andalusian female.
White Minorca male × Blue Andalusian female.

6. Give examples of the following ratios: 9:7, 13:3, 9:4:3, 15:1, and explain how each of these ratios is produced.

7. Assuming that cockerels only are to be used for the production of broilers and roasters, give a list of ten sex-linked crosses that could be made, placing the crosses in the order of their practical importance.

8. A strain of White Plymouth Rocks from year to year contains a few birds with greenish-colored shanks. Give the probable reason for this and explain how to eliminate this undesirable character from the strain.

9. (*a*) If a nonbarred male is mated with a barred female and an F_1 female from this mating is mated with her father and an F_1 male with his mother, what will be the appearance as to barring of the offspring of these two matings?

(*b*) Explain how it is that in the Cambar breed the sex of the chicks can be distinguished at hatching time.

10. What interesting situation exists regarding the feather pattern characters, barring, lacing, penciling, mottling, and spangling in their relation to black pigmentation?

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CHAPTER V

THE INHERITANCE OF MORPHOLOGICAL CHARACTERS

Numerous breeds and varieties of domestic fowl are noted for the beauty and utility of their individual members, beauty sometimes being enhanced by a lovely color pattern, discussed in the preceding chapter, or by some striking morphological character which adds to the attractiveness of the individual.

Morphological characters are those relating to form or size. Breeds and varieties of domestic fowl differ a great deal in regard to structural characters such as the form or shape of comb, the presence or absence of a crest, the length of saddle coverts, presence or absence of feathers on the shanks, number of toes, body form, and many other characters. Two examples of structural or morphological differences in type of feathering are the "silky" feathers of the Silkie breed and the "frizzled" feathering of the Frizzle breed.

The inheritance of a number of morphological characters has been studied and the results as given in the following pages go to show how generally applicable is the principle of Mendelian inheritance to the great majority of characters possessed by domestic fowls

THE INHERITANCE OF SILKINESS

The Silkie breed of fowls is noted for the "silky" appearance of its plumage, this condition being due to the hookless condition of the barbules of each feather. That the Silkie breed is of ancient lineage is attested by the fact that Taubert (1910), in his historical sketch of the breed, traces its lineage back to the time of Aldrovandus in 1600.

According to Jones (1921), there are five varieties of the Silkie breed. Wright (1891) mentions Silkies with single combs and non-feathered shanks, and Sturges (1909) describes blue-feathered Silkies, but whether these should be recognized as distinct varieties is doubtful because it is known that birds with "silky" plumage have appeared occasionally in numerous breeds. Individual specimens with "silky" plumage have appeared from time to time in many breeds in different parts of the world. Bement (1863) mentions "several instances of fowls of this description having sprung from those of the ordinary character." Tegetmeier (1873) mentions silky Cochins, and Jones

(1921) gives several observations of various poultrymen who have recorded the appearance of silky birds in Rhode Island Reds, Black Orpingtons, White Wyandottes and other varieties.

The Gene for Silkiness. Apparently the first reference to the inheritance of silky plumage is that of Darwin (1868), who observed that when Silkies were bred among themselves they produced nothing but silky-plumaged birds, but when Silkies were crossed with birds having normal plumage the F_1 offspring all had normal plumage. Davenport (1906, 1907), Bateson and Punnett (1908), Cunningham (1912), Bonhote (1914), Jones (1921), and Dunn and Jull (1927) studied the inheritance of silkiness and their results taken collectively give in the F_2 generation a total of 207 birds with normal plumage and 64 with silky plumage, expectation on a 3:1 basis being 203.25 to 67.75. The conclusion is justified that silkiness is differentiated from nonsilkiness by an autosomal recessive gene.

The sporadic appearance of birds with silky plumage in breeds and varieties having normal plumage is readily accounted for on the assumption of a mating of two birds each of which has the gene for silkiness in a heterozygous condition.

THE INHERITANCE OF FRIZZLED PLUMAGE

The frizzled plumage character is peculiar to the breed known as Frizzles, the feathers of which curl upwards and forwards because of the absence or modification of the hooklets of each feather, a thickening of its barbules and barbs, and alterations in the direction of the barbules and barbs. The plumage has the appearance of being rubbed the wrong way.

An Old Character. That the frizzled condition of plumage in the domestic fowl has persisted for a long time is borne out by the fact that a frizzled fowl was described by Aldrovandus (1600). From early times frizzled fowls have been reported in many parts of the world, including Java, Ceylon, East India, Southern Asia, Asiatic Russia, West Indies, Philippine Islands, and other parts. Its occurrence in England is reported by Tegetmeier (1867). By Buffon (1799) it was called *le coq frisée* and, according to Dürigen (1923), in Mauritius and Mozambique it was known as the Hurricane Fowl.

The Gene for Frizzling. The genetics of the frizzled plumage character has been studied by Davenport (1906), Crew (1925), Wriedt (1925), Hutt (1930), and Landauer and Dunn (1930*a*). In a cross between a Frizzle fowl and a Silkie, Davenport secured results that showed that the frizzled character was dominant over nonfrizzling. Crew and Wriedt each were led to believe that the frizzled

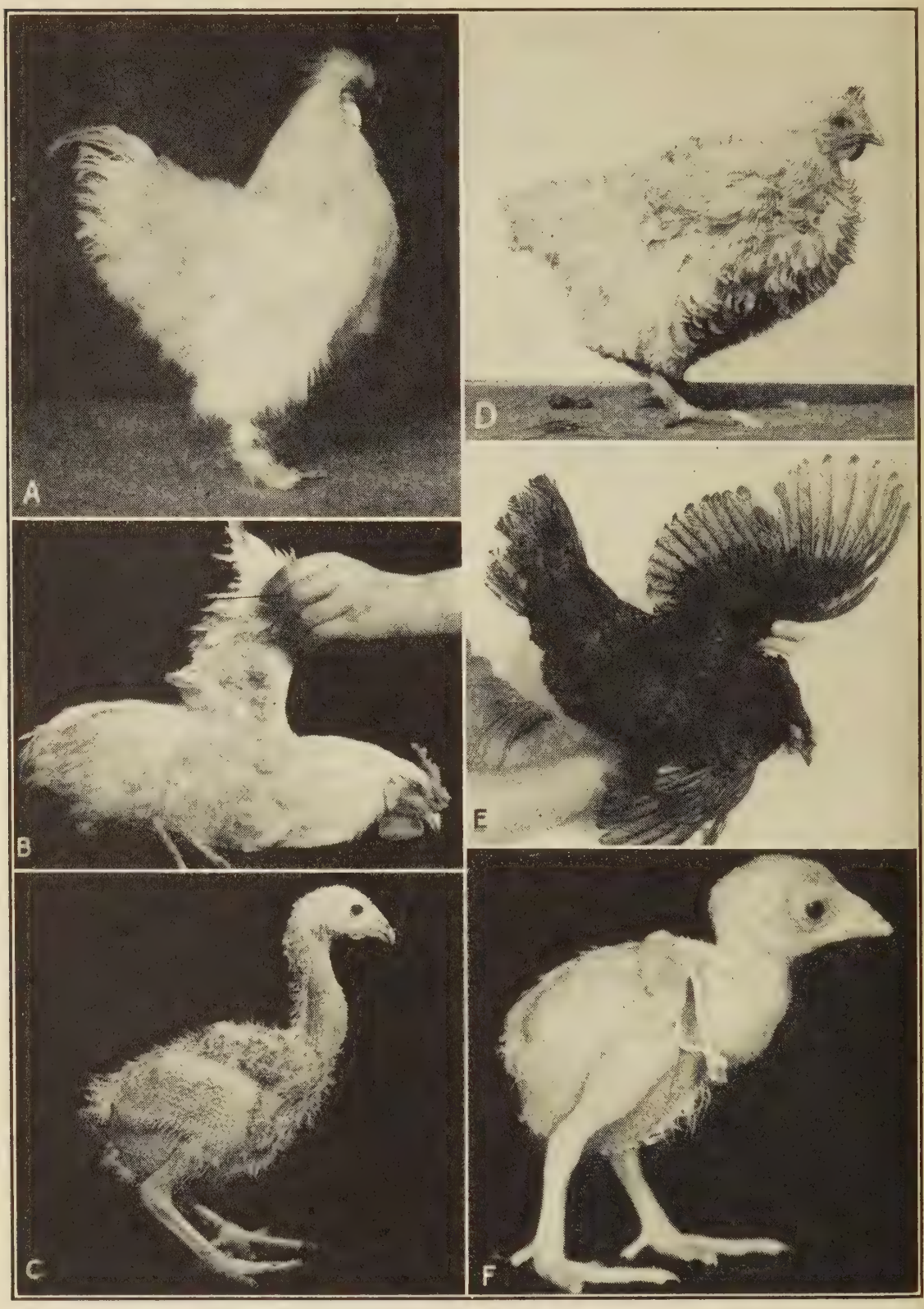


FIG. 35. A, Silkie (U. S. D. A.); B, heterozygous flightless (Warren); C, homozygous flightless (Warren); D, homozygous frizzled (Landauer); E, frayed wing feathers (Warren); F, naked (Hutt).

character acts as a lethal in a homozygous condition, but this has been shown not to be the case by Hutt and by Landauer and Dunn.

In certain matings Hutt determined that he had secured two kinds of frizzled birds, one group with "ordinary" frizzling and one group with "extreme" frizzling. Five females with ordinary frizzling were mated to a White Leghorn male and produced 33 birds with ordinary frizzling and 29 with normal plumage. Five females with extreme frizzling were mated to the same White Leghorn male and produced 48 birds, all of them having ordinary frizzling. The five females with ordinary frizzling were heterozygous, and the five females with extreme frizzling were homozygous, for the frizzling character.

The results which Landauer and Dunn (1930*a*) secured confirm the observations of Hutt (1930), although the former make a distinction between what they call two types of heterozygous frizzles. One type they call "exhibition-type" heterozygous frizzling and the other "ordinary-type" heterozygous frizzling, the difference in frizzling being due to more conspicuous structural changes in the feathers of the exhibition-type birds. Landauer and Dunn observed that the exhibition-type of heterozygous frizzling is the kind of frizzling that private breeders exhibit at poultry fairs and that it "has been produced by selection and that it depends in its expression upon the presence of other genes beside the gene for frizzling."

The difference between frizzling and nonfrizzling is due to an autosomal gene, frizzling being incompletely dominant. The homozygous type of frizzling is more extreme than the heterozygous type. Hutt (1932, 1936) and Landauer (1933) have reported the existence of a recessive gene that modifies frizzling, this modifier apparently being widely distributed among various breeds. Birds that are homozygous for frizzling and homozygous for the modifier lack the extreme curliness of the feathers that characterizes homozygous frizzles that do not have the modifier. Birds that are heterozygous for frizzling and homozygous for the modifier, although showing typical frizzled feathering in the definitive feather stage, resemble normal plumaged birds as adults.

THE INHERITANCE OF "FRAYED" FEATHERING

Warren (1938) has reported the inheritance of a variation in feather structure termed "fray," a condition not recognizable at hatching time. In the wing and tail feathers of the adult, however, there is a defective condition of the barbules, resulting in an imperfect locking of the anterior and posterior barbules. The separated barbs

give the frayed appearance of the vanes of the feathers. The condition is due to an autosomal recessive gene.

THE INHERITANCE OF "FLIGHTLESSNESS"

A peculiar condition which causes the flight feathers of the wing and some of the other large feathers to break off when subjected to slight pressure has been described by Warren (1932). New feathers that follow the molt also break off as soon as they are sufficiently mature to become dry. Only the base of the shaft and the quill of the flight feathers remain. Marlow and Caldwell (1934) have demonstrated certain chemical and structural differences between "flightless" and normal feathers: normal feathers contained 22.7 per cent more cystine sulfur but less than one-half as much phosphorus as "flightless" feathers, and X-ray analyses showed the "flightless" feathers to be of abnormal structure.

A heterozygous "flightless" male when crossed with normal females produced progeny one-half of which were flightless and one-half normal, indicating that "flightlessness" is due to an autosomal dominant gene.

Mayhew (1934) has reported the appearance of flightless birds resembling in many respects those observed by Warren but matings of Mayhew's flightless birds to normal ones produced normal birds only.

Warren (1937), on the basis of further matings with his "flightless" birds, observed that in a homozygous condition the flightless gene gives rise to birds that appear normal at hatching time, but at about four weeks retarded feather growth appeared with the result that as adults they were almost nude of feathers and the beak and toe nails were quite fragile. Flightless birds mated to flightless birds produced progeny consisting of 116 flightless, 51 normals, and 16 featherless. Backcross matings of flightless to normal feathering gave approximately a 1:1 ratio, indicating that the flightless condition is heterozygous. The flightless gene in homozygous condition is apparently usually lethal, approximately two-thirds of the homozygous individuals dying, as indicated by the proportion of 116:51:16 indicated above.

THE INHERITANCE OF "NAKEDNESS"

Chicks completely free of down at hatching time have been reported at different times. Serebrovsky and Petroff (1929) observed three such chicks among 16,000 and from an analysis of the pedigrees of these three abnormal chicks concluded that a recessive mutation had

ccurred. Warren (1930) reported that, among downless chicks that ame under his observation, the condition was not inherited.

Hutt and Sturkie (1938) have described a type of downlessness n a strain of White Leghorns which is due to a recessive sex-linked nutation. At hatching time, the chicks vary from almost complete ownlessness to almost normal down-covered chicks, the majority eing very sparse of down. The anterior portion of the chick is usually nore naked than the posterior end and what few feathers are present ppear as strands due to failure of the barbs to separate. Nakedness s most noticeable from about two to four weeks of age, while in the dult stages, the degree of nakedness varies considerably. There are eathers on all the pterylae and there are down feathers in the apteria. The remiges, or wing feathers, as well as many of the rectrices, or tail eathers, are usually missing. Areas lacking plumage are covered vith stubs of feathers or swollen follicles. The feathers that are resent are normal in structure, except that in many cases, the apical arbs and the tips of the rachis are broken off and some of the barbs re unusually long and lack barbules.

F_1 males produced naked chicks just as readily when mated to nrelated females as when mated to full-sisters, all the naked chicks eing females, although approximately one-half of the affected embryos ied during the last three days of incubation. From six matings of F_1 nales mated to normal females, 958 chicks either hatched or developed p to 18 days of incubation, of which 712 were normal and 206 were aked, a close approximation to a 3:1 ratio. In the case of three of hese six matings, the sex of all hatched chicks was determined, there eing 239 normal males, 104 normal females, and 134 naked females. Among the normal chicks, the ratio of males to females was approximately 2:1. From two matings of heterozygous males mated to naked emales there were 43 normal: 41 naked died during the last three days f incubation or hatched and among these 41 naked ones, there were 6 males and 25 females. Hatchability data indicated no differential nortality between naked and normal embryos up to 18 days of incubaion but much greater mortality among naked embryos than among normal embryos during the last three days of incubation, the percentage mortality being 46.7 and 8.5, respectively. Mortality from hatching time up to six weeks was about 13 per cent for normal chicks and about 55 per cent for naked chicks.

THE INHERITANCE OF "HENNY-FEATHERING"

Among the various American standard breeds of chicken, the Campines and Sebright Bantams are known as "hen-feathered" breeds,

inasmuch as in these breeds the male hackle and saddle feathers are of the same shape, color, and relatively the same length as in the female. The observation of Morgan (1919, 1920) and Punnett and Bailey (1921) go to show that hen-feathering is dominant to cock-feathering. Jull and Quinn (1930) were led to believe that modifying genes are involved.

It has been pointed out in Chapter II that the difference in plumage between cock-feathered and hen-feathered breeds is due to a difference in the reactivity of the skin structures to the stimulus resulting from the presence of the gonad, henny-feathering in Campine and Sebright males being due to the genetic constitution of these breeds.

Punnett (1937) has suggested that henny-feathering may be accounted for by assuming that the character is due to a dominant gene, *H*, the effects of which are possible only when the gene is activated by a testicular hormone. The reaction between the gene and the hormone inhibits the production of typical cock-feathering. In birds genetically *hh* the hormone has no effect on the plumage. Punnett suggests that since *H* behaves in inheritance as an autosomal dominant, it was originally carried on the sex chromosome but by dislocation became attached to an autosome.

THE INHERITANCE OF COMB FORM

One of the most easily recognized structural or morphological differences existing among breeds and varieties is in the form or shape of the comb. In Chapter I it has been pointed out that there are single combs, rose combs, pea combs, walnut combs, V-shaped combs, leaf combs, and others.

Genes for Comb Form. The inheritance of comb form, particularly as it applies to single, rose, pea, and walnut combs, has been studied intensively, and the results have brought to light a very interesting situation.

The results of the experiments of Bateson (1902), Hurst (1905), Davenport (1906), Bateson and Punnett (1908), and Dunn and Jull (1927) in crossing rose-comb birds with single-comb birds show that rose is dominant over single on a monohybrid basis, the F_2 generation segregating in the proportion of 3 rose to 1 single. It is well known, however, that there are different kinds of rose combs; the spike of the Wyandotte rose comb bends downward whereas the spike of the Hamburg rose comb projects straight outwards. Punnett (1923) observes that there are probably genes responsible for the particular type of rose comb common to a breed or variety, but this matter has never been investigated.

When Silkies were crossed with White Leghorns, it was found hat all the F_1 birds had the Silkie type of rose comb, the majority aving three points. The F_2 generation consisted of 139 birds with he Silkie type of rose comb and 32 birds with single combs. There vas no indication that the truncated or multiple-point condition of he Silkie type of rose comb is inherited as a separate character.

In crosses between birds having pea combs and birds having single ombs, Bateson (1902), Davenport (1906), and Bateson and Punnett (1908) have shown that pea comb is dominant to single comb on a nonohybrid basis, the F_2 generation segregating in the proportion of 3 pea to 1 single. Punnett (1923) points out that although some of he heterozygous pea combs are more or less single combs, the fact hat they are really pea combs is made clear when birds possessing hem are mated to birds having rose combs.

A very interesting situation was found to exist in the inheritance of comb form when rose-combed birds were crossed with pea-combed birds. The results showed that all the F_1 birds had walnut combs, an uncommon form. The nonappearance of rose comb and pea comb n the F_1 and the appearance of only walnut combs shows that the genes for rose and pea act upon each other to produce a new type of comb.

Since rose comb is dominant to single on a monohybrid basis, the symbol *R* is used to designate the rose-comb character; and since pea comb is also dominant to single on a monohybrid basis, the symbol *P* is used to designate the pea-comb character. When a rose-combed and a pea-combed bird are mated together each has the recessive allelomorph of the other so that a rose-comb bird would be *RRpp* and a pea-comb bird would be *rrPP*. The F_1 birds would be *RrPp*, which is the walnut type of comb.

When the F_1 birds having walnut combs are mated among themselves, both the males and the females produce the four kinds of gametes, *RP*, *Rp*, *rP*, and *rp*. The mating of these four kinds of F_1 gametes produces an F_2 ratio of 9:3:3:1, a result to be expected when F_1 birds differ in two pairs of genes. The F_2 ratio consists of 9 birds with walnut combs, 3 birds with rose combs, 3 birds with pea combs, and 1 bird with a single comb, as shown in Fig. 36.

It is clear, therefore, that the walnut type of comb is the result of the interaction of the genes *R* and *P*, and the combination of the recessive allelomorphs, *rr* and *pp*, produces the single type of comb.

A Pea and Walnut Inhibitor. In a large number of matings involving the pea comb, Petroff (1929) observed a deficiency of pea combs in several of the matings. Combs were classified by their

phenotypic appearance, and in this connection the observation of Punnett (1923), referred to previously, might explain why Petroff observed a deficiency of pea combs, for according to Punnett some birds heterozygous for pea comb might be mistaken for birds having single combs. The results of certain individual matings convinced Petroff, however, that certain of his birds carried a gene which inhibited the development of pea and walnut combs.

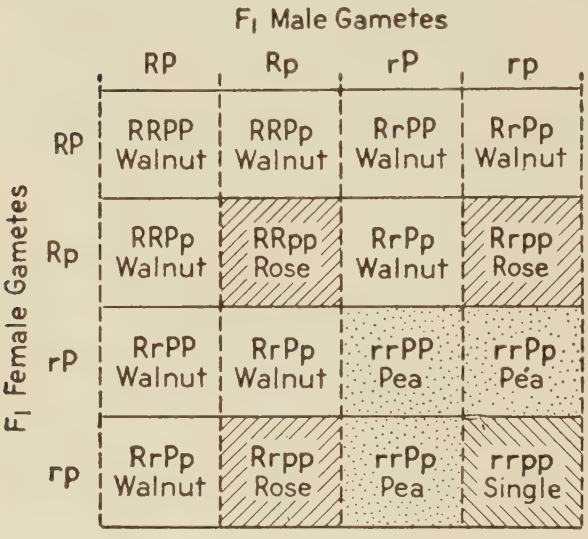


FIG. 36. Showing the F_2 results secured from an original cross of rose comb × pea comb. The F_1 birds have walnut combs, due to the interaction of the gene *R*, for rose comb, and the gene *P*, for pea comb. When the F_1 birds (*RrPp*) are mated among themselves an F_2 ratio of 9 walnut : 3 rose : 3 pea : 1 single is the result.

The Inheritance of Side-Sprigs. A side-sprig, which is a well-defined, pointed growth on the side of a single comb, is regarded as a disqualification, as stated in Chapter I. Punnett (1923) points out that side-sprigs occur also on rose combs, although in such cases the defect is not regarded by exhibition breeders as of such a serious nature as to disqualify a bird. Punnett was led to believe that side-sprigs were dominant to the absence of side-sprigs.

The inheritance of side-sprigs in Single-Comb White Leghorns has been investigated by Asmundson (1926), who concluded that side-sprigs are due to the interaction of two dominant autosomal genes which are complementary in their action, so that when both are present either in the heterozygous or homozygous condition side-sprigs are produced.

Warren (1939) observed a variation in the form of the blade of the comb in Single-Comb Rhode Island Reds, the blade being spike-like in structure similar to that found on rose combs. The spike-blade was recognizable only at maturity and was found to be more prevalent among females than males. The results secured from reciprocal matings indicated absence of sex linkage. It was concluded that the major gene giving rise to spike-blade is recessive, with a tendency toward incomplete dominance of the normal type of single comb.

THE INHERITANCE OF CREST

Several breeds and varieties, including the Silkie, Houdan, and some of the Polish varieties, are noted for the development of a crest

of feathers surmounting the head. Krautwald (1910) says that the crest occurs in the frontal region of the skull, is present in the chick, and is inherited.

Hurst (1905), Davenport (1906), Cunningham (1912), Bonhote (1914), and Dunn and Jull (1927) secured results which demonstrate that the presence of a crest is due to an autosomal dominant gene. The size of the crest is apparently due to multiple genes.

In the crested Polish breeds the frontal bones of the skull are raised into a dome-shaped protuberance, giving rise to a condition known as cerebral hernia, one of the first illustrations of which was given by Darwin (1868). The results of recent research indicate that cerebral hernia is homozygous crest.

THE INHERITANCE OF MUFFS AND BEARD

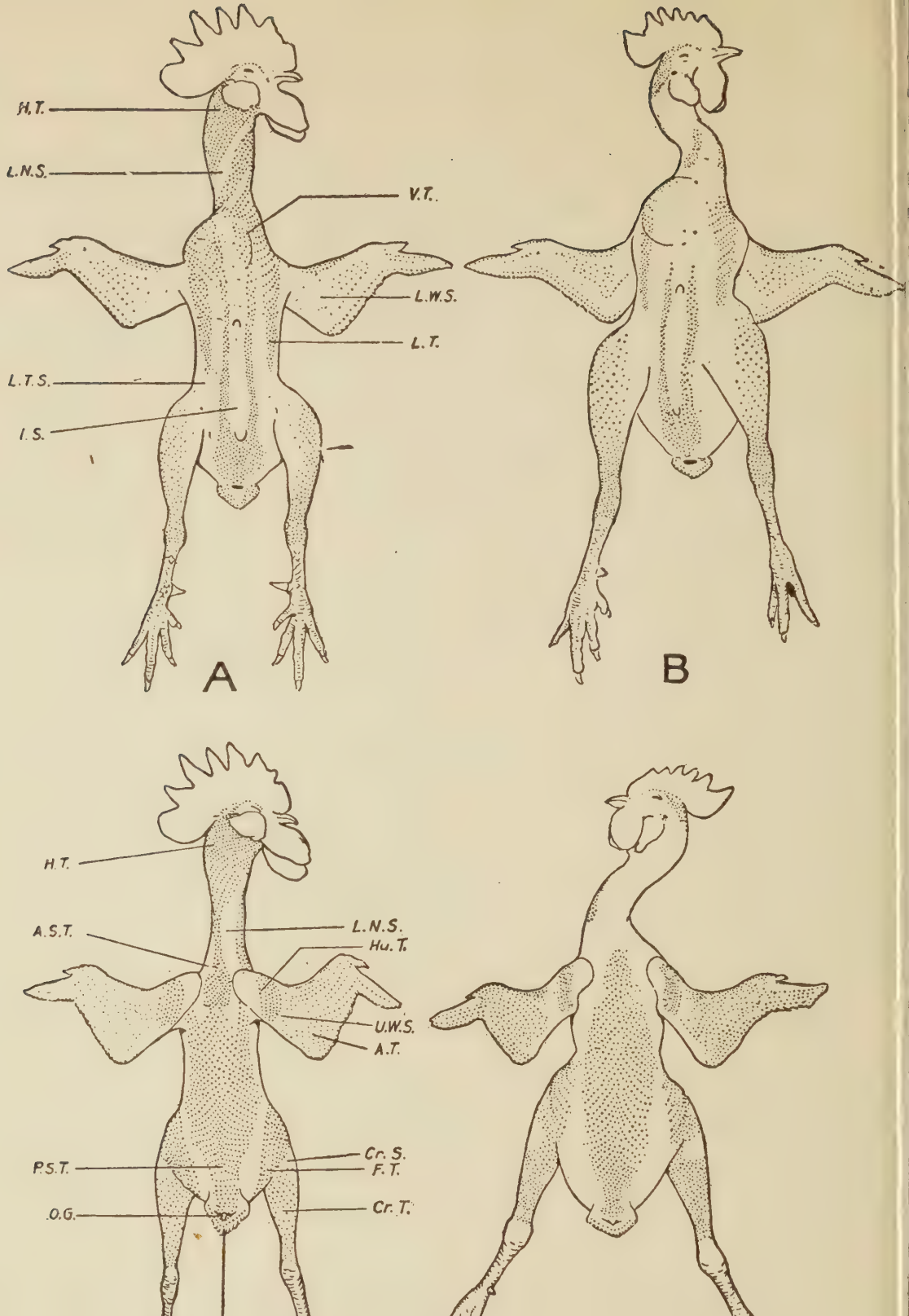
These peculiar structural characters, common to certain continental breeds, have apparently been studied but very little. Davenport (1906) found that, when the Mottled Houdan was crossed with the White Leghorn as well as with the Black Minorca, all the F_1 birds had muffs and beard. When F_1 birds were backcrossed to White Leghorns, the progeny consisted of those with and those without muffs and beard in nearly equal numbers. The muffs and beard character is apparently dominant to absence of muffs and beard on the basis of a single autosomal gene.

THE INHERITANCE OF THE NAKED-NECK CHARACTER

There is one breed of fowl that differs from all other breeds in having no feathers on most of the neck. By some this breed is known as the "Transylvania Naked-Neck"; by Crew (1922) and Greenwood (1927) it has been called the "Hackless" fowl; and by Punnett (1923) and others it has been referred to as the "Bare Neck" fowl. A Naked-Neck male is shown in Fig. 38.

According to Wright (1891), this breed with such a peculiar structural deficiency originated in Transylvania, but birds with this character are now found in many parts of the world.

Not only are neck feathers absent but the area of skin lacking the feathers becomes loose, thickened, wrinkled, and deep red in color during the period of sexual activity. A careful examination of naked-neck birds has been made by Greenwood (1927), who observes that these birds have an incomplete covering of feathers, "the contour feathers of the head, neck, trunk, and limbs being restricted to more or less elongated narrow bands between which the skin is either naked or clothed only with down." The feathered bands have been called feather tracts or pterylae by Nitzsch (1867), and the intervening naked



KEY TO LETTERING OF FIGURES

A.T.	Alar Tract.	*L.N.S.*	Lateral Neck Space.
A.S.T.	Anterior Spinal Tract.	*L.T.*	Lateral Tract.
Ca.T.	Caudal Tract.	*L.T.S.*	Lateral Trunk Space.
Cr.S.	Crural Space.	*L.W.S.*	Lower Wing Space.
Cr.T.	Crural Tract.	*O.G.*	Oil Gland.
F.T.	Femoral or Lumbar Tract.	*P.S.T.*	Posterior Spinal Tract.
H.T.	Head Tract.	*U.W.S.*	Upper Wing Space.
Hu.T.	Humeral Tract.	*V.T.*	Ventral Tract.
I.S.	Inferior Space.		

FIG. 37. The feather tracts on the ventral side, A, and on the dorsal side, C, of the normal fowl and the feather tracts on the ventral side, B, and on the dorsal side, D, of the Naked-Neck fowl. (Greenwood.)

ands have been called apteria. The illustration in Fig. 37 shows the xtent to which normal and naked-neck birds differ concerning the eather tracts; Greenwood (1927) has further noted that in the naked-eck fowl the apteria were naked in all regions of the body, having o down or semiplumes like the apteria of normal birds.

The suggestion by Taubert (1910), Duerst (1911), and others that he naked-neck character is acquired is not supported by evidence. On the other hand, the evidence submitted by Greenwood (1927) nakes it clear that the peculiar character is of genetic origin, arising probably as a mutation. Moreover, the breeding experiments of Davenport (1914) and Crew (1922) show that the naked-neck char-acter behaves as a simple dominant to normal feathering, an autosomal gene being responsible for its development.

THE INHERITANCE OF "CROOKED-NECK" CHARACTER

In a study of the inheritance of hen-feathering in Brown Leghorns at the U. S. Animal Husbandry Experiment Farm, Beltsville, Mary-and, there appeared seven birds with decidedly crooked necks in one of the matings in 1926. A bird with this defect is illustrated in Fig. 38. The simultaneous appearance of seven such abnormal birds in one mating led to an analysis of the results, and it was found by Jull and Quinn (1931*a*) that these abnormal birds were produced by three different dams in a total population of 39. It became apparent at once that not only was the crooked-neck condition inherited but also that it was probably inherited on a monohybrid basis. Subse-quent matings demonstrated such to be the case, the autosomal gene producing the condition being recessive.

THE INHERITANCE OF CLOSE FEATHERING

Certain breeds, such as the Cornish and Games, have short feathers that lie close to the body; certain varieties, such as Brahmas and Cochins, have feathers that do not lie close to the body, giving such birds what is termed profuse plumage.

In crosses between close-feathered breeds and others, it has been found that close-feathering is dominant. Bateson (1902) crossed what were then known as Indian Game (Cornish) with White Leg-horn and observed that the F_1 progeny were close-feathered. Morgan crossed Game Bantams with Sebright Bantams and secured similar results. Punnett (1923) crossed the Aseel male with Brown Leghorn females and observed that the F_1 birds were as close-feathered as the Aseel male parent. Wassina (1926) crossed Indian Game (Cornish) with the Pavloff bantam and found that the F_1 birds were close-

feathered and that the F_2 birds indicated that segregation had taken place on a simple monohybrid basis.

INHERITANCE OF SHANK FEATHERING

The information given in Table 1 in Chapter I shows that several breeds and varieties have feathered shanks as one of their characteristics. Brahmas, Cochins, Langshans, and other breeds have feathered shanks, although it should be noted that some breeds differ from others in the amount or extent of shank feathering. Cochins, for instance, have much more profuse shank feathering than Langshans.

The Genes for Shank Feathering. Although Hurst (1905), Davenport (1906, 1909), Cunningham (1912), Morgan and Goodale (1912) and Bonhote (1914), studied the inheritance of shank feathering, their results are inconclusive. Punnett and Bailey (1918), however, secured results that permitted drawing rather definite conclusions. They crossed Croad Langshans with Hamburgs and with Brown Leghorns and noted that the F_1 birds were shank feathered, but not so heavily as the Croad Langshan parents, and that the F_2 segregated into a 3:1 ratio of birds with feathered and nonfeathered shanks. The results they secured led them to conclude that shank feathering is dominant to absence of shank feathering, an autosomal gene being involved.

On the other hand, Punnett and Bailey concluded that two autosomal genes are responsible for the feathering in those breeds having more profuse shank feathering than their Croad Langshans. The results which Dunn and Jull (1927) secured in crosses between Silkies and White Leghorns, Brown Leghorns, and White Plymouth Rocks led to the conclusion that the Silkie should be added to the group of birds with profuse shank feathering, two dominant autosomal cumulative independent genes being responsible for the shank feathering as found in the Silkie.

From certain crosses made by Serebrovsky and his co-workers (1927) the same two dominant genes as reported by Punnett and Bailey were found to explain the results satisfactorily. The same was found to be true of crosses made by Lambert and Knox (1929) between Black Langshans and Buff Orpingtons and White Plymouth Rocks. Danforth (1929) crossed a Mille Fleur Bantam male with Golden Sebright Bantam females and reported that the Mille Fleur carries the two genes each in a homozygous dominant condition and that the Golden Sebright carries the two genes each in a homozygous recessive condition.

Lambert and Knox state that probably many Black Langshans are heterozygous for at least one of the two dominant genes.

The Inheritance of Stubs. A stub is described by poultry breeders as the quill portion of a short feather and is regarded as a disqualification when it is present in breeds having nonfeathered shanks. It is well known, however, that stubs occur from time to time in individuals of numerous breeds having nonfeathered shanks. Stubs are usually found on the web of skin between the toes and on the toes although they may sometimes be found on the outer sides of the shanks. Frequently, instead of the quill portion of a feather, down may be present, the amount varying from almost complete absence as observed by the naked eye to a complete covering of the web between the outer toes.

Warren (1930) developed by selection a strain of White Leghorns in which a high proportion of the progeny had down and another strain of White Leghorns in which practically none of the progeny had down. These two strains were crossed and the results showed that the presence of down is "more or less recessive in its behavior" and that more than one autosomal gene is involved.

THE INHERITANCE OF BRACHYDACTYLY AND SYNDACTYLY

By brachydactyly is meant a shortening of the fourth toe so that it is shorter than the second toe, the reverse being the normal condition. By syndactyly is meant a condition in which the third and fourth and sometimes the second and third toes are united by a web.

Aside from the observation of Davenport (1909) that syndactyly is dominant to absence of syndactyly, comparatively little work has been done on either of these two structural peculiarities except some research by Danforth (1919*a*, 1919*b*, 1929). The first suggestion put forward by Danforth (1919*b*) was to the effect that the three structural characters, shank feathering, brachydactyly and syndactyly, are associated in heredity. Warren (1940) has observed, however, that syndactyly is independent of shank feathering and behaves as a recessive. Danforth (1929) suggested that each of the two autosomal cumulative independent genes for shank feathering tends to produce brachydactyly.

That Danforth's hypothesis is probably untenable has been suggested by Lambert and Knox (1929), who make the suggestion that linkage may exist between the genes for brachydactyly and one of the genes for shank feathering. In view of the fact that there are probably more than two genes for shank feathering, Danforth's original suggestion is ruled out and his second suggestion becomes less tenable, particularly in view of the fact that neither brachydactyly nor syn-

dactyly has been observed with any degree of frequency by those who have investigated the inheritance of shank feathering.

THE INHERITANCE OF POLYDACTYLY

By polydactyly is meant the presence of an extra toe or toes. In Table 1, Chapter I, certain breeds are indicated as having five toes on each foot instead of four, which is the number common in most breeds. Among other breeds having five toes are the Houdans and Silkies, the extra toe occurring near the hallux or hind toe.

Several investigations have been undertaken over a period of years with the view of determining the nature of the inheritance of polydactyly, but the results are not very conclusive, so complex has the problem proved to be.

The observations of Bateson (1913), Bateson and Saunders (1902), Bateson and Punnett (1905 and 1906), Hurst (1905), Davenport (1906 and 1909), Barfurth (1908, 1909, 1911), Dunn and Jull (1927), and Punnett and Pease (1929) may be summarized by saying that polydactyly appears to be due to a dominant autosomal gene, but that a four-toed bird may carry the gene for polydactyly and still be four-toed owing to the presence of one or more genes which inhibit the development of polydactylism. Moreover, since the data examined by Punnett and Pease showed that polydactylous birds may also carry the inhibiting gene they suggested that such polydactylous birds also carry one or more genes "rendering possible the manifestation of the polydactylous effect in spite of the presence of the inhibitor."

According to Hutchinson (1931), the results which Punnett and Pease secured may be accounted for by assuming that dominance is controlled by genes, as suggested by Fisher (1928*a*, 1928*b*), and that birds heterozygous for polydactyly but lacking all the genes favoring the dominance of polydactyly are four-toed birds. In other words, Hutchinson's suggestion is to the effect that four-toed birds occurring in the F_1, F_2, and backcross generations secured from a mating of polydactylous and normal birds may be due to a deficiency in one or both parents of genes necessary for the dominance of polydactyly.

THE INHERITANCE OF VULTURE HOCK

Two standard American breeds of chicken, the Sultan and the Mille Fleur Booted Bantam, have vulture hocks as a characteristic of their morphological feathering development and in this respect differ from most other breeds described in the American Standard of Perfection, although there are breeds in Europe with the same characteristic. The long feathers which constitute the vulture hock arise from the

posterior area of the tibial feather tract, above the tibiometatarsal hock) joint.

Jull and Quinn (1931*a*) mated a male with well-developed vulture hocks with a pen of Rhode Island Red females, absence of vulture hocks being a characteristic of this breed, and secured an F_2 generation of 82 birds without vulture hock and 29 birds with vulture hock.

The evidence shows that not only is vulture hock recessive to absence of vulture hock, as Davenport (1906) suggested, but that an autosomal gene is responsible for the development of the character.

THE INHERITANCE OF "LONG TAIL"

The Phoenix and Yokohama fowls of Japan have a very peculiar structural difference from practically all other breeds in that the males of these Japanese breeds have what is called a "long tail." As a matter of fact, however, the extreme length of the tail is due to the very long sickle feathers and saddle coverts in the male, although the main tail feathers in both males and females are longer than in most other breeds. (See Fig. 38.)

Cases have been reported where the sickle feathers of the Yokohama male have attained a length of over 20 feet. The literature dealing with the raising of these fowls makes it apparent that the particular diet given them has something to do with the ultimate length of feather attained, but it is apparent that the character is inherited.

The inheritance of the long tail has been investigated by Davenport (1906) and Bonhote (1914). Davenport crossed the Yokohama and the White Cochin Bantam and the Yokohama with the Dark Brahma and observed that in both crosses the F_1 male birds had saddle coverts, sickle, and main tail feathers much longer than in the Cochin and Brahma parents but not so long as in the Yokohama parents. The same was true of the main tail feathers of the F_1 females. Bonhote crossed the Yokohama and the Silkie and secured similar F_1 results to Davenport's, and in the F_2 generation Bonhote secured 19 birds with long tail and 5 with short tail. These results indicate that the long-tail character is probably due to an autosomal gene, but since the length of the saddle coverts, sickle, and main tail feathers in the F_2 varied considerably, it would appear that multiple genes are probably involved.

THE INHERITANCE OF RUMPLESSNESS

One of the most unique structural variations existing among domestic fowls is the condition known as rumplessness, in which the birds have no tails. (See Fig. 38.) Rumpless fowls seem to have

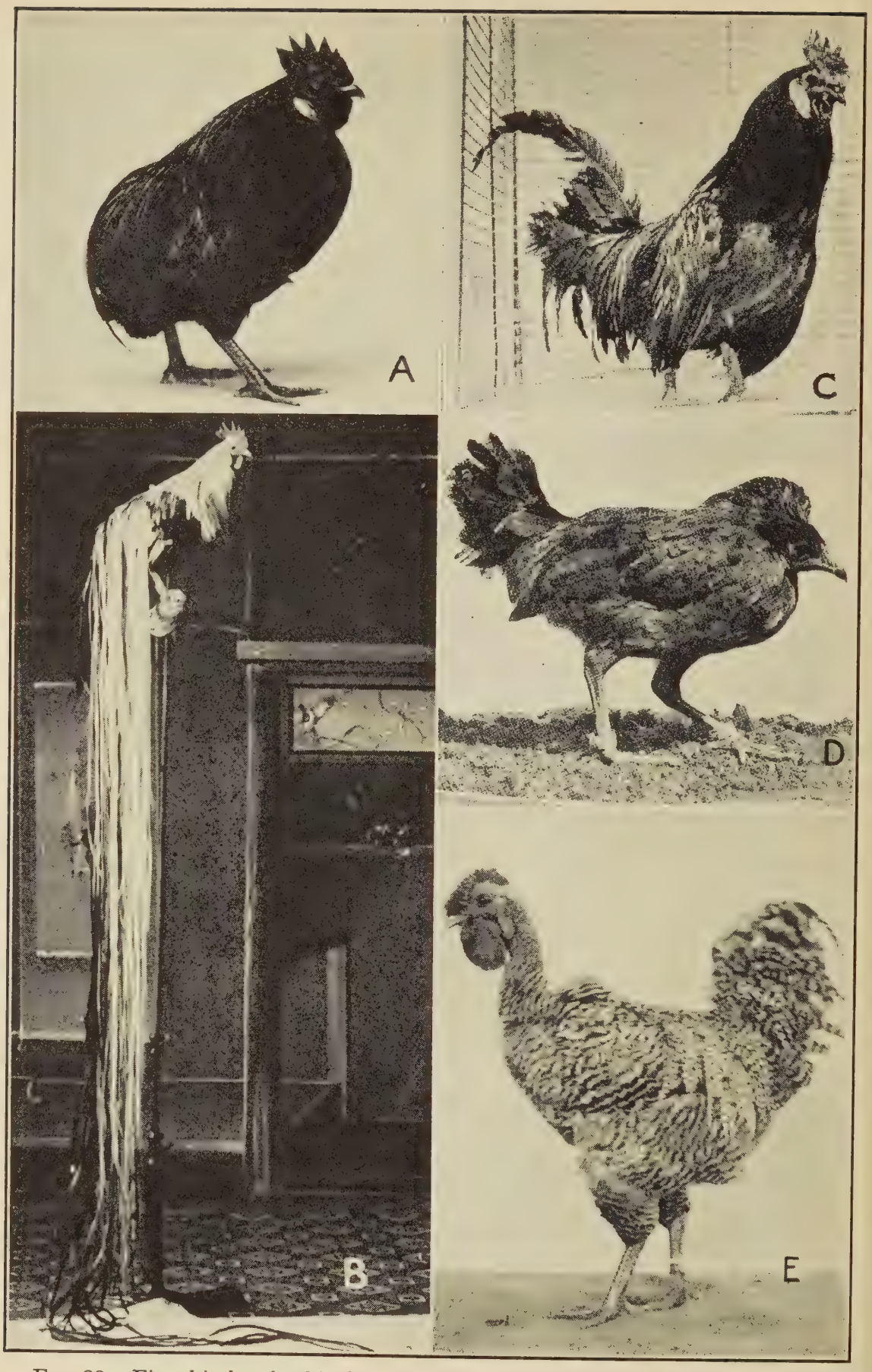


FIG. 38. Five kinds of odd characters that have been found to be inherited in Mendelian manner. A, a rumpless bird (Photo by Ogiwara). B, a "long-tailed" bird. (Photo by Kinugawa.) C, a German Creeper. Note the "squatty" appearance, due to the short legs. (Photo by Landauer and Dunn.) D, a "Crooked-Neck" bird. (Photo by U. S. D. A.) E, a "Naked-Neck" bird. (Photo by U. S. D. A.)

been in existence for hundreds of years, because Tegetmeier (1873) refers to a description of them by Aldrovandus in 1645. The observations of various writers make it appear certain that strains of rumpless birds have been bred for many years in widely scattered parts of the world, including Japan, South America, and many parts of Europe.

Three Types of Rumplessness. The investigations of Landauer and Dunn (1925) and Landauer (1928) have shown that there are three types of rumpless birds. Live specimens of all three types resemble each other more or less closely, but differences among them are manifest from their breeding results, owing to the fact that in one type the trait is not inherited, whereas in the two types in which it is inherited there are differences in morphological structure.

The chief difference between a normal bird and a rumpless one is a deficiency in the latter of parts of the skeleton of the tail, the caudal vertebrae and the pygostyl being absent.

Landauer (1928) has observed, however, that there is an intermediate type of hereditary rumplessness that is somewhat different from the hereditary type that is completely rumpless. In the intermediate type a few tail feathers may be present and the backbones form a graded series from an almost normal condition to an almost completely rumpless condition, the outstanding difference between the intermediate and completely rumpless types being the presence of caudal vertebrae in the intermediate type. In the intermediate type one or two vertebrae of the synsacrum and all except the last two of the vertebrae of the pygostyl are absent.

The Genetics of Rumplessness. The results of investigations conducted by Dunn (1925) led him to conclude that rumpless birds that sporadically appear in various flocks are usually of the non-hereditary type, that is, when mated to normal birds they produce nothing but normal offspring, a result similar to that secured by Davenport (1906).

Dunn also found that other matings of rumpless males to rumpless females produced F_2 progeny in the proportion of 3 rumpless to 1 normal bird. These results indicate the dominance of rumplessness on a monohybrid basis. Furthermore, when this same type of rumpless bird was mated to normal birds, rumpless and normal progeny were produced in approximately equal proportions. These results indicate that the hereditary type of rumplessness usually encountered is in a heterozygous condition. This fact makes it clear why Darwin (1868), Tegetmeier (1873), Dürigen (1886), and Wright (1902), among others, state that strains of rumpless birds produce some normal birds.

In further experiments on the inheritance of rumplessness, Dunn

(1926) discovered that the homozygous rumpless condition is viable; a rumpless female upon being mated to a normal male produced rumpless progeny only, 17 in number. Completely rumpless birds mated to normal birds produced 245 rumpless and 267 normal birds, and intermediate rumpless birds mated to normal birds produced 135 completely or intermediate rumpless and 146 normal birds. Dunn states that the intermediate condition appears to be due to the interaction of the rumpless gene with a partially dominant, independent modifying gene.

Dunn and Landauer (1934, 1936), in further work with their rumpless stock, observed that modifying multiple recessive genes, many of which were homozygous following selection, became effective in changing the proportion of intermediates among all rumpless heterozygotes from 22 per cent in 1926 to 100 per cent in 1935. Complete rumplessness, which at the beginning of their experiments was characteristic of heterozygotes, came to be expressed in the homozygotes only. It was suggested that some of the homozygotes also became modified toward the normal condition, many of the rumpless birds having assumed the intermediate type and complete rumplessness having practically entirely disappeared from the stock. Coincident with this change there was noted also a further modification of the heterozygous type toward the normal. These modifying genes act, therefore, on homozygotes and heterozygotes, on the latter relatively more than on the former. Finally, it was observed that one of the effects of these modifying genes was "to render recessive such harmful effects as rumplessness" and that they also tend to extinguish the homozygous effect of the rumpless mutation.

THE INHERITANCE OF THE "CREEPER" CHARACTER

There are various names for the Creeper Fowl in various countries; in Great Britain they are known as Scotch Dumpies, in France as *Courtes pattes*, and in Germany as *Krüperhuhn*. Investigational work has disclosed, however, that these Creeper fowls in various countries are of the same genetic constitution.

Creepers have two peculiar structural characters that distinguish them from all others. The wings and the legs are very much shortened, the development of the bones of the latter differing markedly from that in normal breeds. (See Fig. 38.) Cutler (1925) points out that all the leg bones are correspondingly shortened, that the tibia is usually bent considerably, and that the fibula is much better developed than in normal birds.

Landauer (1934) has shown that, although the embryos of Creeper

and normal stocks appear to be about the same, after the fourth week of postnatal life Creeper chicks are smaller than normal chicks due to the reduction of long bone length in the Creeper chicks. From the fourth to about the seventh week the Creeper chicks grow relatively faster than normal chicks. Adult Creeper females are less variable than adult Creeper males as far as bone measurements are concerned. It was also found that the reduction in bone length is relatively greatest among the bones that are the latest to be formed during development. This observation was confirmed by Lerner (1936) in connection with his study of heterogonic growth in the posterior limbs of the fowl.

The genetics of the Creeper fowl has been studied by Landauer and Dunn (1930*b*), who used Creepers from America, Germany, Scotland, and the Marquesas Islands. Their very interesting results are explainable on the basis of the Creeper character being determined by an autosomal dominant gene, which in a homozygous condition causes the death of the embryo in the early stages of incubation. Landauer and Dunn found that the characteristic lethal period is at the beginning of the fourth day of incubation, that very rarely does an embryo homozygous for the lethal gene live up to hatching time, and that it never hatches. Their data show that even when the gene is in a heterozygous condition it has a semilethal effect.

The lethal nature of the gene in a homozygous condition is demonstrated by the following facts:

1. Only birds in a heterozygous condition exist. This has been shown to be the case by numerous breeding tests.

2. In matings of Creeper × Creeper there is a segregation of 2 Creepers to 1 normal, giving a 2:1 ratio instead of a 3:1 ratio normally expected if the embryo carrying the gene in a homozygous condition were to live and hatch.

3. Approximately 25 per cent more embryos die during the first six days of incubation in matings of Creeper × Creeper than in matings of Creeper × normal fowls.

A study of the early development of homozygous Creeper embryos by Landauer (1932) led to the observation that the effects of the Creeper mutation are brought about by a general retardation of body growth at the definite stage of development rather than by a specific gene action on those bones which later exhibit reduced length. Homozygous Creepers that develop up to about hatching time exhibit striking malformations of the extremities, which are known as phocomelia, as observed by Landauer (1933). It was pointed out by Fell and Landauer (1935) that "the abnormalities of the phocomelic homozygous Creeper embryos are the result of an unspecific growth-

retarding effect of the Creeper mutational difference at an early stage of development." Landauer (1935) observed numerous peculiar malformations that developed in heterozygous Creeper embryos and in normal embryos that were developed by segregation from Creeper matings. It was concluded that these malformations were not due to the Creeper mutation nor to a recessive gene linked with it, but were apparently due to irregular crossing-over, the rare occurrence of these malformations being due to a partial suppression of crossing-over.

THE INHERITANCE OF OTHER MORPHOLOGICAL CHARACTERS

During recent years research has determined the mode of inheritance of a number of morphological characters that have not been discussed previously. For want of space, the results are presented briefly.

Short Legs in Japanese Bantams. Landauer (1938) has shown that the extremely short legs of the Japanese Bantams are due to the same gene that causes shortening of the legs in the Creeper.

Short Legs in Dark Cornish. The shortness of the extremities in Dark Cornish fowls is due to several genes, probably more than one of which is dominant to normal leg length, according to Landauer (1935). The tibia and tarsometatarsus are markedly affected, whereas the fibula is better developed than in other breeds. One of the genes responsible for the shortening effect is lethal in a homozygous condition, the embryos dying just prior to the end of the incubation period. This lethal mutation is independent of the Creeper mutation.

The Inheritance of Dwarfism. There have been several records of the appearance of dwarfism among the larger breeds of domestic fowl, one of the first of which was that by Landauer (1929) who designated the condition *Myxoedema infantalis*. Among those who have studied the inheritance of dwarfism most extensively are Mayhew and Upp (1932) and Upp (1934). In a flock of Rhode Island Reds there appeared several birds with shortened legs, outer toes turned outwards and backwards, bodies carried in a nearly horizontal position, and, in some, heads that were abnormal. Upp (1934) demonstrated that dwarfism is inherited as a simple autosomal recessive.

Inheritance of Abnormal Osteogenesis. Hutt (1932) observed that the extreme thickening of the tarsometatarsus, with modification of the carpometacarpus and other bones, is inherited as an autosomal recessive.

Inheritance of Abnormal Beaks. A condition described as twisted beaks was found by Hutt (1932) to be inherited as a simple autosomal recessive. In an inbred strain of White Leghorns, Asmund-

son (1936) observed an abnormal condition of the upper mandible, the maxillae being absent or much reduced and the upper mandible being frequently bent to one side. Few of the affected chicks are able to pick the shell. The condition is due to a simple autosomal recessive gene.

Inheritance of Baldness. Hutt (1932) described a condition in which small irregular areas on the top of the head were entirely devoid of feathers, this condition being apparently due to a simple autosomal recessive gene.

Inheritance of Double Oil Gland. There is usually only one oil or uropygial gland in the fowl but Hutt (1932) observed birds with two oil glands, a single dominant gene being responsible.

Inheritance of Spurlessness. Goodale (1925) observed that the spurred condition in females was due to an autosomal recessive gene. Kozelka (1933) observed a condition of spurlessness in a strain of White Leghorns and found that it was inherited as a simple autosomal recessive.

Inheritance of Kidney Abnormality. Jeffrey, Beaudette, and Hudson (1937) described a condition of kidney abnormality in a strain of White Leghorns in which the left kidney was either atrophied or missing entirely, the condition being inherited; the mode of inheritance, however, was not determined.

THE INHERITANCE OF BODY FORM AND SIZE

It is well known that some breeds differ greatly in their general appearance, Game breeds having an entirely different build of body from Cochins, Langshans differing materially from Wyandottes, and Leghorns from Orpingtons; then there are the bantam breeds that are greatly reduced in size as compared with the "normal-sized" breeds.

It is true, of course, that much of the difference in the external appearance of birds belonging to different breeds is accentuated by the feather contour, so that, although two breeds may appear to be very different in body conformation, when stripped of feathers their bodies may be indistinguishable. Then again, two breeds having similar standard weights may appear to be quite different in size because of the position in which the body is carried, the Single-Comb Black Minorca being much more upright in carriage than the Plymouth Rock. It should be noted still further that although there are standard weights for most of the breeds, there is great variability in body size among the males and among the females of each breed. In view of these considerations, it is quite apparent that determination of the

mode of inheritance of body form and size is an extremely complicated problem.

Schneider and Dunn (1924) observed that body weight is from three to six times more variable than bone measurements and that in males the humerus, ulna, femur, and tibiotassus were 16 per cent longer than in females. Latimer (1927) observed a difference of about 20 per cent between the sexes in the lengths of these bones, and Hutt (1929) observed that in males these bones were 13.4 per cent longer than in females.

Among some of the first investigations on the inheritance of body form in the domestic fowl were those of Kopeć (1927) who crossed White Leghorns with Buff Orpingtons. It was observed that the Buff Orpingtons had longer tibiotarsi and tarsometatarsi than the White Leghorns and that the length of these bones in the hybrids more nearly approached the long-boned parent. Ghigi and Taibell (1927) observed that in an Indian Game $\times$ Leghorn cross the tarsi of the F_1 generation were of the same length as that of the longer-boned parents. Latimer (1927) found that the rate of the growth of the leg bones in the fowl is higher than the rate of body-weight growth and that the male bones increase from hatching time to maturity to a greater extent than do female bones, with the exception of the femur, in which case no difference in rate of growth was observed. Lerner and Asmundson (1932), in matings of Ancona $\times$ Light Sussex, observed that up to twelve weeks of age there was a significant difference in the length of the tarsometatarsi between the two types of backcross progeny in favor of the Light Sussex $\times$ F_1 mating. Hutt (1935) found that in White Leghorns the greatest difference in bone length between the sexes was in the tarsometatarsus.

Maw and Maw (1935) made the observation that considerable variation appears to exist in body conformation within the general-purpose breeds, such as Plymouth Rocks and Rhode Island Reds. Jaap and Penquite (1938) concluded that differences in the conformation of live birds may be expressed accurately by comparing body weight, shank length, keel length, and minimum anterior body depth. In females the growth of the length of the shanks ceases at five months and in males at six months. It was also observed that different visual conformation groups of dressed birds differ significantly in the relation between the cube root of their body weight and the following four linear measurements: shank length, keel length, anterior body depth, and width of breast, the breast measurement of which was found to be 1.5 inches from the anterior end of the keel on a line toward the

insertion of the femurs. The relation between shank length and body weight was found to be the most suitable single criterion of market conformation quality in live birds.

Maw and Maw (1938) and Jaap and Thompson (1940) observed that the body of the sire is transmitted to his progeny. In their studies on heritable differences in adult female body conformation, Jaap and Thompson were not able to demonstrate any consistent relation between proportional length of shank and keel and proportional anterior body depth. The shape as well as the location of the keel in its longitudinal axis were found to have more influence on the conformation of dressed birds than the length of the keel. In breeding for uniformity of body conformation, it is suggested that considerable improvement should result from the selection of breeding stock on the basis of the relationship between shank length and body weight.

It is quite obvious that the final shape which the fowl's body assumes is determined, for the most part, by the sum total of the growth of the different parts of the body, the rates of growth of different parts perhaps being at different levels at various stages in the development of the bird.

Rensch (1923), in an excellent review of size inheritance in the domestic fowl, observed that the difference in size between "normal-sized" breeds and bantams and differences in size among the various "normal-sized" breeds is due to differences in cell size as well as in cell number. According to Bucciante (1929), chick embryos have a rather definite number of cells at particular morphological stages, regardless of the time required to reach those stages. On the other hand, Keller (1933) was of the opinion that differences in size among the breeds of fowl was due to differences in the size of the cells.

The relation of breed to the rate of growth in chick embryos was investigated by Byerly (1930), who studied eggs from matings of Single-Comb White Leghorns, Single-Comb Rhode Island Reds, and reciprocal crosses between these two varieties. It was found that up to the tenth day of incubation, the White Leghorn and crossbred embryos were heavier than the Rhode Island Red embryos. After the tenth day, however, the Rhode Island Red embryos and crossbred embryos became heavier than the White Leghorn embryos in most cases. Yet the chicks from the four different sources weighed approximately the same at hatching time.

Byerly was led to conclude that differences in size of embryos of the same age and from eggs of the same size, regardless of breed, are slight, and that, although Rhode Island Red and crossbred embryos

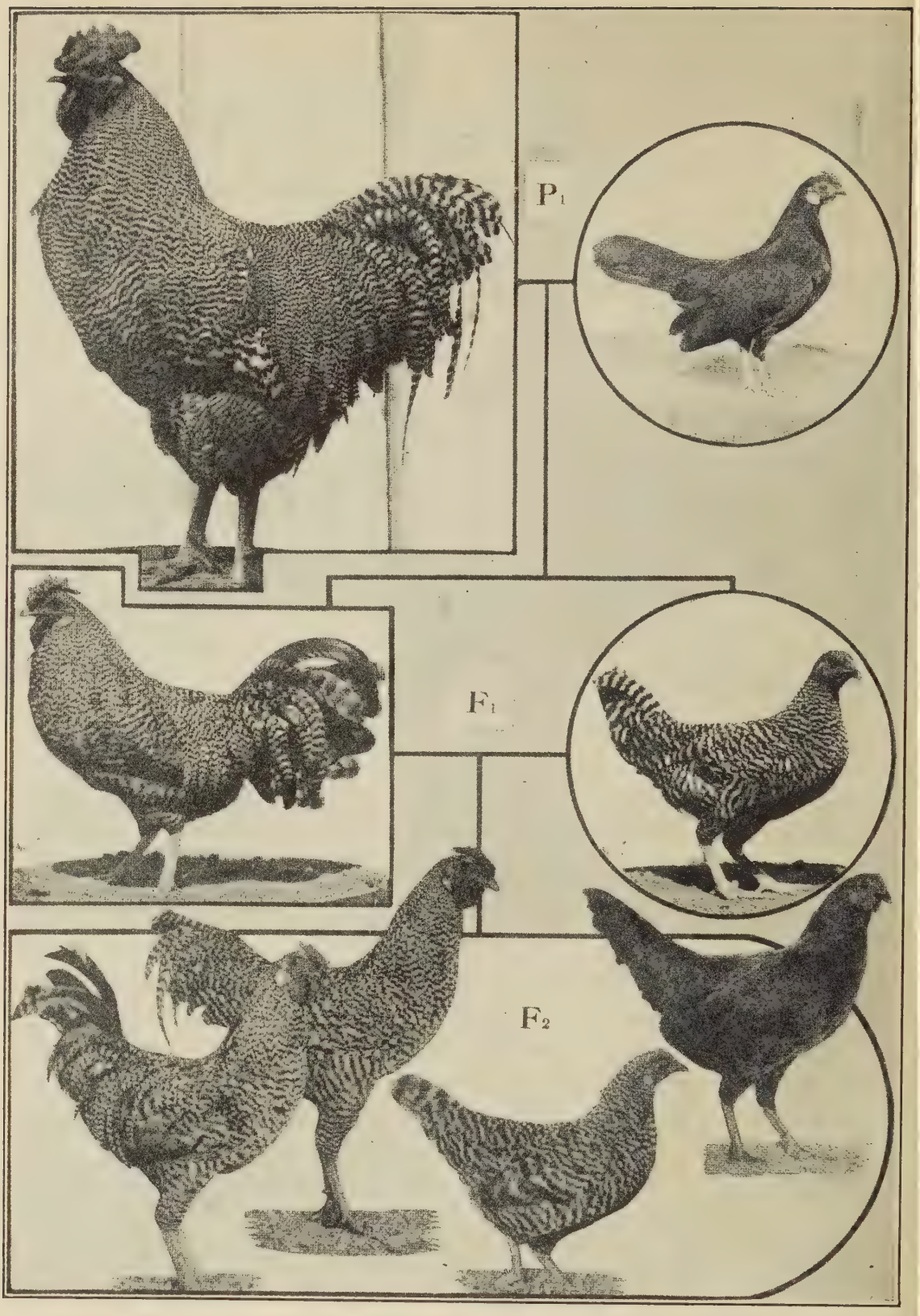


FIG. 39. Photographs of three generations of fowls in a study of the inheritance of body weight. The original cross consisted of Barred Plymouth Rock males × Black Rose-Comb Bantam females; these P_1 birds differed so much in size that artificial insemination was practiced. The F_1 birds were intermediate in size. In the F_2 generation neither of the extremes of parental body weight were secured, indicating that several genes are involved in the inheritance of body weight. The results secured in this cross show that barring is dominant to nonbarring, the F_1 males and females being barred, and in the F_2 generation there are 3 barred birds to 1 black bird but all F_2 males are barred whereas one-half of the F_2 females are barred and one-half are black. (Jull and Quinn, 1931.)

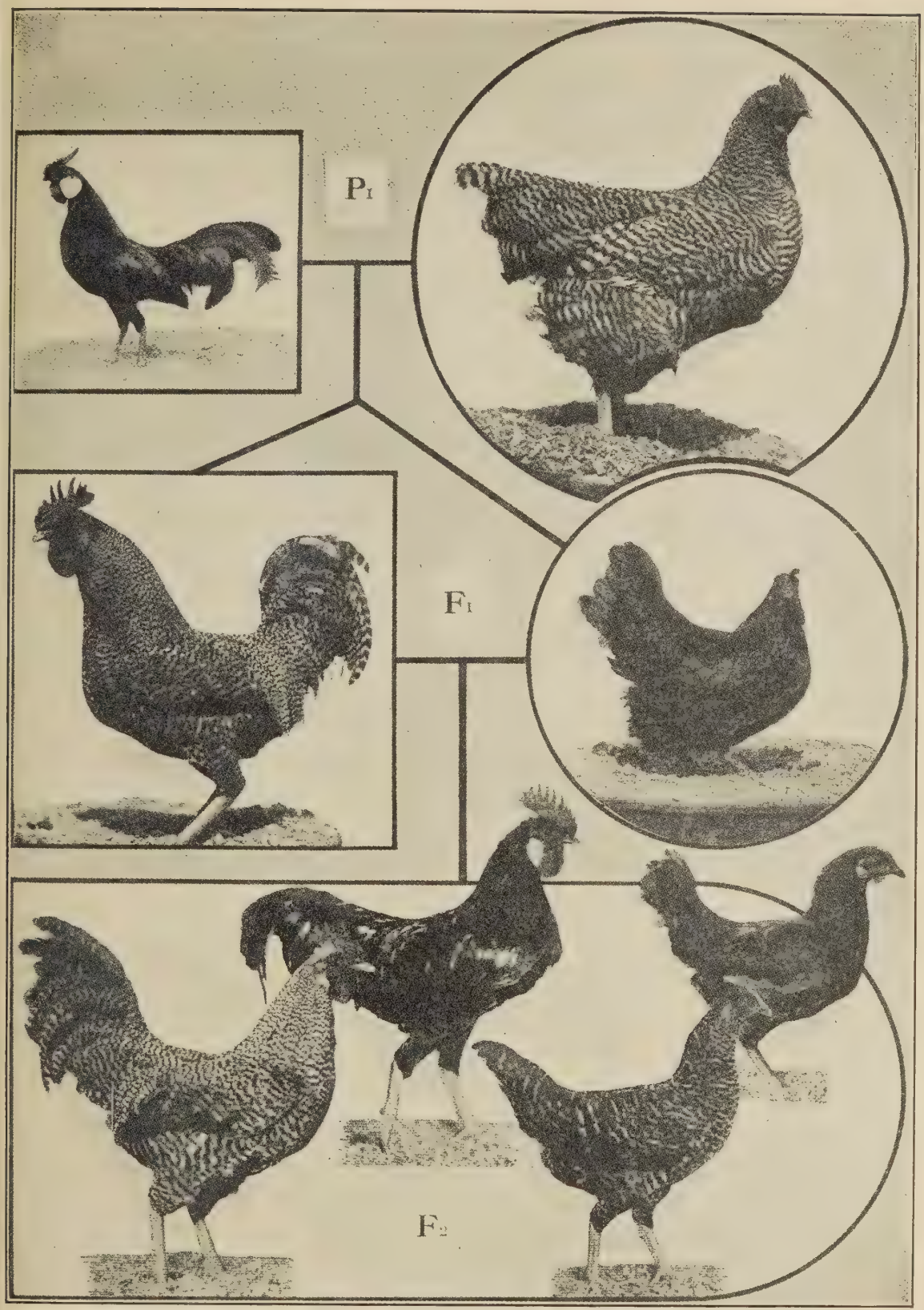


FIG. 40. Photographs of three generations of fowls in a study of the inheritance of body weight. The original cross consisted of Black Rose-Comb Bantam males × Barred Plymouth Rock females, artificial insemination being practiced. The results secured were similar to those secured in the reciprocal cross, illustrated in Fig. 39. From the standpoint of plumage color inheritance, the results secured in this cross demonstrate the sex-linked inheritance of the gene for barring. The Barred Plymouth Rock female parent transmits barring to her sons only and in the F_2 generation one-half of the males are barred and one-half are black, and one-half of the females are barred and one-half are black. (Jull and Quinn, 1931.)

are somewhat heavier than White Leghorn embryos during the latter half of the incubation period, this difference decreased by hatching time, owing to the limitation of food. Henderson (1930), in studies on the embryo growth of White Leghorns, Dark Cornish, and their reciprocal crosses, also observed little, if any, constant significant differences in the growth rates of the embryos. Moreover, Kaufmann (1930*a*, 1930*b*) found that the rate of growth in pigeon and fowl embryos is the same.

On the other hand, Castle and Gregory (1931) showed that crossbred embryos grow faster than purebred embryos. Early differential rates of growth among various breeds were established by Lerner and Asmundson (1932) and Asmundson (1933). Blunn and Gregory (1935) observed that the rate of cell proliferation was relatively greater in the larger sized breeds of fowl than in the smaller sized breeds. Based on the fact that glutathione stimulates cell proliferation, Gregory, Goss, and Asmundson (1935) and Gregory, Asmundson, and Goss (1936) demonstrated that the glutathione values were correlated positively with the rate of cell proliferation at 14 days of incubation and that the glutathione concentration in Barred Plymouth Rock embryos was slightly, but consistently, greater than in White Leghorn embryos from 5 to 19 days of incubation. It was further observed that glutathione concentration was correlated with post-hatching growth rates and adult body weights.

The problem of the inheritance of adult body size has been the subject of numerous investigations, the results of which appear to demonstrate that there are many genes involved in determining the size of the body as a whole and other genes that have a particular effect on certain parts. Among the foremost exponents of this view has been Wright (1918, 1932), whose statistical analysis of the bones of inbred White Leghorns developed by Dunn (1928) led to the conclusion that inheritance of bone length was due primarily to genes having a general effect on size.

Sinnott and Dunn (1935), in their extensive review of the effect of genes on the development of size and form, came to the conclusion that a relatively large number of genes is involved in size inheritance. Schkljar (1935) arrived at a similar conclusion.

That some genes exercise specific effects on certain parts of the body is obvious from the previous discussion in this chapter on the inheritance of different morphological characters. For example, the length of leg in the Creeper fowl as well as in the Dark Cornish have been found to be due to specific genes. These may be regarded as

exceptional cases, however, as far as the problem of size inheritance in its general aspects is concerned.

Studies on size inheritance in the domestic fowl have been undertaken by a number of investigators, and, although the results differ with respect to certain details, there is general agreement that a large number of genes is involved. Those who may be interested in the research problems involved should consult the reports by Ghigi (1909), Punnett and Bailey (1914), May (1925), Sokolov (1926), Ghigi and Taibell (1926), Kopeć (1927), May and Waters (1927), Komdyrev (1928), Danforth (1929), Warren (1930), Jull and Quinn (1931), Waters (1931, 1934), Lerner and Asmundson (1932), Axelsson (1933), Zorn and Krallinger (1934), Lauth (1935), Maw (1935), and Lerner (1937*a*, 1937*b*), who has presented an excellent review of the whole problem.

In practically all cases in which there was not an extreme difference between the sizes of the parental breeds that were used in the original cross, the size of the F_1 progeny was about midway between the parental breed sizes or slightly nearer the larger sized breed. In those cases in which there were extreme differences between the sizes of the parental breeds crossed, as in the case of the Barred Plymouth Rock $\times$ Rose-Comb Bantam matings made by Jull and Quinn (1931) and the Light Brahma $\times$ Golden Sebright Bantam matings made by Maw (1935), the size of the F_1 progeny was slightly nearer the smaller sized breed.

In all crosses from which an F_2 generation was secured there was greater variability in the F_2 than in the F_1 generation.

The results secured from these numerous investigations are for the most part in general agreement in demonstrating that the inheritance of adult body size is dependent upon many genes. It should be noted, however, that Maw (1935) observed that in crosses between Light Brahmas and Golden Sebright Bantams a sex-linked gene was involved in size inheritance. Maw concluded that the skeletal dimensions of the fowl are apparently determined by a number of genes whose effects are of a general nature.

Evidence of sex-linkage in the inheritance of body size is indicated in the results secured from such crosses as those made by May (1925), Warren (1930), Knox and Olsen (1938), and Knox (1939). The F_1 females secured from each of the reciprocal crosses differed materially in weight. At the same time, it is to be noted that in crosses in which the male parent was of the larger parental breed and the female parent was of the smaller parental breed, the F_1 males

were usually larger at ten weeks of age and later than F_1 males secured from reciprocal crosses. Table 13, which shows data by Godfrey (1939), from reciprocal crosses between White Leghorns and Jersey Black Giants, are representative of the results secured by several investigators. Two sets of reciprocal crosses were made, one involving noninbred White Leghorns and the other involving inbred White Leghorns.

TABLE 13. AVERAGE MATURE BODY WEIGHT IN GRAMS OF MALE AND FEMALE PROGENY SECURED FROM RECIPROCAL CROSSES BETWEEN WHITE LEGHORNS AND JERSEY BLACK GIANTS

(Godfrey, 1939)

	Weight of Parents		Weight of Progeny	
	Male	Female	Male	Female
White Leghorn ♂ × Jersey Black Giant ♀	2,025	3,324	2,784	2,267
Jersey Black Giant ♂ × White Leghorn ♀	4,111	1,748	2,942	2,529
Inbred White Leghorn ♂ × Jersey Black Giant ♀	1,889	3,270	2,818	2,201
Jersey Black Giant ♂ × Inbred White Leghorn ♀	4,324	1,522	2,879	2,358

Lerner (1937*b*), in an extensive survey on size inheritance, came to the conclusion that the basic genetic complex for the type of growth of parts of the body with respect to the growth of the body as a whole is common to the different breeds of poultry, with the exception of bantams. Reciprocal matings were made between Barred Plymouth Rocks and Black Minorcas, the results secured indicating that growth gradients exist in the leg bones, the center of growth lying at the distal end. Lerner found that the growth of the femur is hypogonic in relation to the growth of the entire leg, whereas in the tibiotarsus and tarsometatarsus the growth is hypergonic in relation to total leg growth. Among these three leg bones, the femur is the first to be formed and grows at the slowest rate, and the tibiotarsus and tarsometatarsus grow at approximately the same rate. Lerner (1937*a*) observed that the length of the shank (tarsometatarsus) in live birds is a good index of inherent body size. Lerner (1939) observed that shank length and body weight are more closely correlated in growing birds than in mature ones.

TABLE 14. DOMINANT AND RECESSIVE MORPHOLOGICAL CHARACTERS IN CHICKENS

Character	Dominant or Recessive	Autosomal or Sex-Linked
Rose comb	Dominant to single comb	Autosomal
Pea comb	Dominant to single comb	Autosomal
Walnut comb	Dominant to rose, pea, and single	Autosomal
Side-sprigs	Dominant to normal comb	Autosomal
Crest	Dominant to absence of crest	Autosomal
Muff and beard	Dominant to absence of muff and beard	Autosomal
Naked-neck	Dominant to normal neck feathering	Autosomal
Feathered shanks	Dominant to nonfeathered shanks	Autosomal
Vulture hock	Recessive to normal hock	Autosomal
Long tail	Incompletely dominant to normal tail	Autosomal
Hen feathering	Dominant to normal feathering	Autosomal
Frizzle plumage	Incompletely dominant to normal plumage	Autosomal
Silkie plumage	Recessive to normal plumage	Autosomal
"Frayed" feathers	Recessive to normal feather development	Autosomal
Close feathering	Dominant to loose feathering	Autosomal
Flightless	Dominant to normal wing	Autosomal
"Nakedness"	Recessive to normal	Sex-linked
Rumplessness	Dominant to normal condition	Autosomal
Crooked neck	Recessive to normal neck	Autosomal
Dwarfism	Recessive to normal	Autosomal
Creeper condition	Dominant to normal condition, lethal when homozygous	Autosomal
Short Cornish leg	Dominant to normal leg length	Autosomal
Abnormal osteogenesis	Recessive to normal tarsometatarsus	Autosomal
Deformed mandible	Recessive to normal mandible, lethal when homozygous	Autosomal
Abnormal beaks	Recessive to normal	Autosomal
Parietal baldness	Dominant to normal	Autosomal
Spurlessness	Recessive to normal	Autosomal
Polydactyly	Dominant to four-toed condition	Autosomal
Syndactyly	Recessive to normal	Autosomal
Double oil gland	Dominant to normal	Autosomal

PROBLEMS

1. A poultry breeder breeds White Wyandottes only and finds that a few of his chicks have single combs. Suggest matings that will enable him to detect and eliminate the breeders that are heterozygous for rose comb.

2. A White Silkie with its rose comb is mated to a Single-Comb White Leghorn. Using the symbols *RR* for rose comb, *rr* for single comb, *NN* for normal plumage, and *nn* for silky plumage, give the genotypes and phenotypes produced in the F_2 generation.

3. The same mating is made as in Problem 2, and the same symbols are used for rose and single comb and normal and silky plumage, and in addition the symbols *IICCOO* designate the dominant white of the White Leghorn and *iiCCoo* the recessive white of the Silkie, as explained in the preceding chapter. Give the genotypes and phenotypes produced in the F_2 generation.

4. Two males, No. 1 and No. 2, are mated to two females, No. 3 and 4. All four birds have frizzled plumage and pea combs. Male No. 1 with both females produces offspring all of which have frizzled plumage and pea combs. Male No. 2 with female No. 3 produces offspring all of which have pea combs, but some have normal plumage and some have frizzled plumage. Male No. 2 with female No. 4 produces offspring all of which have frizzled plumage, but some have single combs and some have pea combs. Use the symbols *FF* for frizzle plumage, *ff* for normal plumage, *PP* for pea comb and *pp* for single comb and give the genotypes of the two males and the two females.

5. What is the most effective method for the poultry breeder to employ in eliminating side-sprigs and stubs from his flock of White Plymouth Rocks or any other variety with single combs and nonfeathered shanks?

6. Suggest the possible origin of the three following characters: cerebral hernia, muff and beard, and hereditary rumplessness.

7. A male homozygous for both rose comb and the naked-neck character is mated to a female homozygous for both pea comb and vulture hocks. Describe the appearance of the F_1 progeny and show by appropriate symbols for the different characters whether or not there would be produced in the F_2 a bird with a single comb, normal neck plumage, and absence of vulture hocks.

8. In each of the following crosses, what will be the comb character of the progeny produced?

RRpp	× *rrPP*	*RRpp*	× *rrPp*
RrPp	× *RrPp*	*RRPp*	× *rrPp*
RrPp	× *Rrpp*	*Rrpp*	× *Rrpp*
rrPp	× *RrPp*	*rrPp*	× *Rrpp*

9. (*a*) Do poultry breeders experience difficulty in maintaining uniform weights among all individuals of the same breed and variety? If so, explain why.

(*b*) Give an account of the probable origin of the small size of the various bantam breeds.

10. Give the proportion of birds of different body weights produced in the F_2 generation from two crosses in each of which two pairs of weight genes are involved, in one cross the genes having a cumulative effect on weight and in the other cross the genes not having a cumulative effect.

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CHAPTER VI

THE INHERITANCE OF PHYSIOLOGICAL CHARACTERS

Studies involving the inheritance of various physiological characters are of great importance from the practical standpoint because the results secured have an economic bearing on the efficiency with which flock replacements are made and on the income obtained from the flock. Hatchability, viability, rate of feathering, rate of growth, flesh production, and egg production are inherited, but the genetic evidence to date indicates that most of the hereditary variations that exist with respect to each of the characters are determined by a large number of genes.

The larger the number of genes involved in the inheritance of a particular character, the greater the difficulty in determining the mode of inheritance. Moreover, environment frequently plays an important part in the full development of the various physiological characters, the genes sometimes being unable to exercise their full effects. For instance, although the genes for high hatchability may be present, hatching results may be very disappointing because of faulty methods of incubation. Then again, the genes for rapid growth may be present, but the rate of growth attained may be slow because of an improperly balanced diet.

Although the mode of the inheritance of these physiological characters has not been determined, the results of various lines of research have been very fruitful in indicating numerous steps that may be taken to achieve the desired results. The discussion of the inheritance of egg production and egg characters is reserved for separate chapters.

THE INHERITANCE OF HATCHABILITY

By the term "hatchability" is meant the ratio of the number of chicks that hatch to a given number of fertile eggs when presumably ideal conditions of incubation prevail. Hatchability is expressed in terms of a percentage; when 21 out of 25 fertile eggs set from one hen hatch, that hen is said to have a hatchability of 84 per cent.

The fact that hatchability is inherited was first indicated by Gowell (1903), who observed great variability among hens in the hatchability of their eggs. Pearl and Surface (1909) measured the

ariability and secured evidence showing that hatchability is inherited. amson and Card (1920) concluded that individual differences among ens was the most important cause of variation in hatchability. This as confirmed by Dunn (1921, 1922), who also found (1923*a*) that eriodicity of embryo mortality is inherited, some strains showing a elatively high rate of mortality during the early period of incubation, hereas other strains showed a relatively high rate during the latter tages of incubation.

Hays and Sanborn (1924), from correlation studies on the hatchbility of Rhode Island Red eggs, concluded that a hatchability of 5 per cent or more is due to a dominant gene *H*. Birds having a atchability of from 55 to 84 per cent were said to be of the constiution *Hh*, and birds having a hatchability of less than 55 per cent ere said to be of the constitution *hh*. The gene *H* was reported to ave a cumulative effect. This was apparently the first attempt to xplain the inheritance of hatchability on a strictly Mendelian basis.

Jull (1931) pointed out, however, that the low values found by Hays and Sanborn, himself, and others for hatchability correlations etween parent and offspring groups indicate clearly that the inheritnce of hatchability can hardly be explained on the monofactorial basis. This observation was confirmed by Bronkhorst (1933). With ut one gene responsible for high hatchability, a relatively high corelation should result between the hatchability of dams and daughters. If the suggestion of Hays and Sanborn were correct, hens homozygous for high hatchability mated to males also homozygous for high hatchbility should produce exclusively high-hatching daughters, which Snyder (1930) and Bronkhorst (1933) observed, however, was not always the case.

Age of Breeders and Hatchability. Hays (1928) observed that in two series of experiments involving Rhode Island Reds the hatchability of the eggs produced by females mated to males as yearlings was better than the hatchability of the eggs produced by females mated to the same males as cockerels. Jull (1935) secured the results given in Table 15 from matings of yearling females mated to cockerels and to the same birds as yearlings.

The results given in Table 15 show that hatchability was better in the case of the White Leghorn yearling sires than in the White Leghorn cockerel sires but that in the case of the Rhode Island Reds, there were no consistent differences. However, since none of the differences is significant, it is apparent that the age of the sire has little, if any, influence on hatchability.

TABLE 15. PER CENT HATCHABILITY OF EGGS SECURED FROM YEARLING DAMS MATED TO WHITE LEGHORN AND RHODE ISLAND RED SIRES AS COCKERELS AND YEARLINGS

(Jull, 1935)

Breed	Sire No.	Per Cent Hatchability	
		Cockerel Sire	Yearling Sire
White Leghorn	34	59.6	75.0
White Leghorn	41	61.4	77.5
White Leghorn	43	68.1	76.2
Rhode Island Red	127	65.3	67.8
Rhode Island Red	173	73.9	83.5
Rhode Island Red	330	79.0	74.6
Rhode Island Red	334	73.4	77.3
Rhode Island Red	338	83.1	75.8

The hatchability of eggs laid during the first and second laying years has received considerable attention. Stewart and Atwood (1909) found that White Leghorn hens two and three years old gave better results than pullets, and Pearl and Surface (1909) found that yearling Barred Plymouth Rock hens gave slightly though not significantly better results than pullets. Kempster (1921) found that White Leghorn hens gave slightly better results than pullets. In a group of 253 Rhode Island Reds that were bred as pullets and as yearlings, Hays and Sanborn (1924) found that the average hatchability in the pullet year was 56.8 and in the yearling year 47.9. Greenwood (1931–32) found that pullets and yearling females gave practically the same results, whereas three-, four-, and seven-year-old birds gave lower hatchability. More extensive data have been submitted by Axelsson (1932*a*), Hyre and Hall (1932), Funk (1934), Warren (1934), and Jull (1935), the essential data being summarized in Table 16.

The results given in Table 16 show that in every case except one the hatchability of pullet eggs was higher than that of the yearlings, but it should be noted that in not a single case was the difference in hatchability between pullet and yearling eggs significant. Since in the majority, if not in all, cases different males were used with the pullets and yearlings, it is interesting to consider the results secured in the hatchability of the eggs of birds used as pullets and again as

TABLE 16. PER CENT HATCHABILITY OF THE EGGS OF PULLETS AND YEARLINGS AS REPORTED BY VARIOUS WORKERS, THE DATA OF HYRE AND HALL, WARREN, AND JULL BEING FOR THE SAME BIRDS MATED AS PULLETS AND AS YEARLINGS

Axelsson, 1932*a*, *A*; Hyre and Hall, 1932, *H*; Funk, 1934, *F*; Warren, 1934, *W*; Jull, 1935, *J*)

Breed or Cross	Pullets	Yearlings
Rhode Island Reds, *A*	76.0	69.5
Barnvelders, *A*	61.4	50.7
White Leghorns × R. I. Reds, *A*	60.6	57.5
White Leghorns × Barnvelders, *A*	55.2	52.5
R. I. Reds × Barnvelders, *A*	54.4	53.1
White Leghorns, *H*	54.3	52.4
Heavy Breeds, *H*	49.1	52.1
White Leghorns, *F*	82.9	74.5
Rhode Island Reds, *F*	78.9	70.7
Barred Plymouth Rocks, *F*	61.7	57.4
White Plymouth Rocks, *F*	75.9	69.2
White Leghorns, *W*	70.1	62.7
White Leghorns, *W*	75.0	65.8
Rhode Island Reds, *W*	55.0	43.9
Rhode Island Reds, *W*	60.0	53.3
White Leghorns, *J*	79.8	73.9

yearlings when mated to the same males both years. The results of such matings are given in Table 17.

TABLE 17. PER CENT HATCHABILITY OF THE EGGS OF WHITE LEGHORNS AS PULLETS AND AS YEARLINGS MATED TO THE SAME MALES BOTH YEARS

(Warren, 1934)

Pen No.	Pullets	Yearlings
78	66.8	62.4
79	69.2	56.5
80	67.4	54.0

The results given in Tables 16 and 17 show that regardless of whether or not the females as pullets and as yearlings are mated to the same or different males, hatchability tends to be lower in the yearling year.

The fact that hatchability tends to decline still further in the third and subsequent breeding years of birds is clearly shown by the data

TABLE 18. PER CENT HATCHABILITY OF THE EGGS OF BIRDS BRED IN THEIR YEARLING AND SUBSEQUENT YEARS AS REPORTED BY VARIOUS WORKERS

(Hyre and Hall, 1932, *H*; Martin and Insko, 1934, *M*; Warren, 1934, *W*; and Jull, 1935, *J*)

Breed	Age of Female Breeders		
	2nd Year	3rd Year	4th Year
White Leghorns, *H*	62.4	53.2	——
White Leghorns, *H*	61.9	54.8	46.3
White Leghorns, *H*	63.1	58.6	57.3
White Leghorns, *M*	65.8	58.5	60.1
White Leghorns, *W*	65.8	70.0	——
White Leghorns, *W*	76.7	65.6	——
White Leghorns, *W*	78.0	72.4	60.7
Rhode Island Reds, *W*	53.3	49.2	——
Rhode Island Reds, *W*	64.1	62.5	——
Rhode Island Reds, *W*	69.2	65.8	54.2
White Leghorns, *J*	72.3	68.6	——
Rhode Island Reds, *J*	76.9	73.0	——

in Table 18. It should be noted that with the exception of the data of Martin and Insko, the same females were used in the yearling and subsequent years.

In connection with the data given in Table 18, it should be stated that in practically no case is the difference in hatchability between any two years significant. Nevertheless, in every case except one, the third year hatchability is lower than the second year hatchability, and in every case except one the fourth year hatchability is lower than the third year hatchability.

It seems possible to conclude that hatchability declines slightly as the breeding females grow older. The reason for this, whether it be of a physiological nature or otherwise, apparently has not been determined.

Hatchability of Dams and Daughters. One way to study the relationship between the hatchability of dams and that of their daughters is by the correlation technique. In employing this method, Hays and Sanborn (1924) found that the correlation coefficient in the case of 811 Rhode Island Reds was 0.20 ± 0.02; Jull (1931) found that the correlation coefficient of the hatchability of 74 Rhode Island Red dams and their 148 daughters was 0.21 ± 0.05 and that for 60 White Leghorn dams and their 105 daughters the correlation coefficient

was 0.16 ± 0.06; Bronkhorst (1933) found that the correlation coefficient in the case of 1,142 White Leghorns was 0.18 ± 0.02. These correlations are of a low order but indicate a significant influence of dams on the hatchability of their daughters' eggs. In other words, dams whose eggs are of high hatchability tend to transmit this character to their daughters and, likewise, dams whose eggs are of low hatchability tend to transmit this character to their daughters, although considerable variation is to be expected in both cases.

The fact that such is the case has been demonstrated clearly by the results secured by Jull (1931) who divided the dams into two groups depending upon whether or not the hatchability of their eggs was above or below the mean for the group as a whole and then compared the mean hatchability of the eggs of the daughters of each group of dams. The pertinent data are given in Table 19, the two Rhode Island Red groups of dams including those with a hatchability of 68 per cent or better and those with a hatchability of less than 68 per cent, and the White Leghorn groups of dams being classified according to whether their hatchability was above or below 74 per cent. In the case of each breed, the same males were mated to several dams in both groups, and similar males were also mated to daughters of both groups of dams, so that the influence of the males on hatchability was not a factor.

Table 19. Hatchability of Rhode Island Red and White Leghorn Dams and Their Daughters, Classified According to the Mean Per Cent Hatchability of the Dams

(Jull, 1931)

Breed	No. of Dams	Mean Per Cent Dams' Hatchability	No. of Daughters	Mean Per Cent Daughters' Hatchability
Rhode Island Red	51	80.6	105	75.1
	23	59.9	43	66.4
White Leghorn	36	81.2	62	63.4
	24	64.4	43	52.3

The data given in Table 19 show that in the case of both Rhode Island Reds and White Leghorns the dams with the higher mean hatchability produced daughters whose eggs hatched significantly better than those of the daughters of the dams whose hatchability was

below the mean of the whole group. This simply means that high hatchability dams tend to transmit high hatchability to their daughters and vice versa.

The Influence of the Male. As Landauer (1937*c*) has pointed out, in order to make a test of the role of the male in the inheritance of hatchability, it is necessary to make indirect comparisons such as the hatchability of dams and daughters of the same sires, dams and mates, mates and daughters, sires' mates and sons' mates, or first- and second-year daughters of the same males.

The data given in Table 20 include the principal results secured in the correlation studies that have been made.

TABLE 20. COEFFICIENTS OF CORRELATION IN HATCHABILITY INDICATING THE INFLUENCE OF THE MALE IN THE INHERITANCE OF HATCHABILITY

(Data compiled by Landauer, 1937*c*)

Coefficient of Correlation between	Investigator	No. and Breed	Coefficient
Dams and daughters of same males	Hays and Sanborn	748 Rhode Island Reds	0.06 ± 0.02
	Bronkhorst	1,061 White Leghorns	0.09 ± 0.02
Dams and mates of same males	Hays and Sanborn	647 Rhode Island Reds	0.16 ± 0.03
	Bronkhorst	1,079 White Leghorns	0.13 ± 0.02
Mates (average) and daughters of same males	Hays and Sanborn	412 Rhode Island Reds	0.23 ± 0.03
First- and second-year daughters of same males	Hays and Sanborn	51 Rhode Island Reds	0.30 ± 0.09
Sires' mates and sons' mates	Hays and Sanborn	170 Rhode Island Reds	0.08 ± 0.05

With respect to the coefficients of correlation given in Table 20, it is interesting to note that the correlations are of a relatively low value, and, when considered in relation to the influence of the female on hatchability, the male has relatively less influence.

Inbreeding Effects on Hatchability. Inbreeding is the mating of relatives. Since there are degrees of relationship, such as full-brothers and full-sisters, aunts and nephews, uncles and nieces, first cousins, and tenth cousins, so there are degrees of inbreeding. The mating of males to their full-sisters and females to their full-brothers is the closest form of inbreeding that can be practiced.

Cole and Halpin (1916) found that during three years of full-brother × full-sister matings of Rhode Island Reds the hatchability decreased from 67 to 18 per cent. No particular attention was paid to hatchability in the selection of the breeding stock each year, so another experiment, also with Rhode Island Reds, was undertaken in which the breeders were selected each year on the basis of hatchability,

viability, and egg production. Cole and Halpin (1922) report that after a few generations hatchability declined to such an extent that the experiment was discontinued. Similar results were secured by Goodale (1927) with White Leghorns. Although Wreidt (1927) secured good results on inbreeding White Leghorns, the degree of inbreeding, however, was not very high.

Dunn (1923, 1928) inbred different families of White Leghorns, and, although he found that in all inbred strains hatchability decreased perceptibly, there were differences among the families with respect to the degree of the decrease in hatchability. The combined results secured from four families are given in Table 21.

TABLE 21. DECLINE IN HATCHABILITY AS THE RESULT OF CONTINUED INBREEDING

(Dunn, 1928)

Generation	Inbred Families		Noninbred Families
	Number of Families	Percentage of Hatchability	Percentage of Hatchability
P_1	8	75.0	
F_1	8	50.5	40.3
F_2	7	46.7	67.5
F_3	5	34.3	60.8
F_4	2	46.8	60.1
F_5	1	41.5	59.2

The results given in Table 21 show that there was a decline both in the number of inbred families and in hatchability. Landauer (1937*c*) states that the apparent rise in hatchability in the fourth and fifth generations is due to the survival of one family with a relatively high hatchability.

A decline in hatchability following close inbreeding has also been reported by Warren (1927–28, 1934), Jull (1929*a*, 1929*b*), Dumon (1930), Dunkerly (1930), the British Ministry of Agriculture and Fisheries (1934), Byerly, Knox, and Jull (1934), and Vecchi (1936). Only the more pertinent data need be given here to show the general trend. Jull (1929*a*) reported the following percentages of hatchability in parental and in full-brother × full-sister matings of Barred Plymouth Rocks for three generations: 76.2, 42.6, 44.6, 23.2. In similar

matings of White Leghorns, Jull (1929*a*) reported the following percentages of hatchability: 82.5, 61.5, 51.2, 48.2.

In Table 22 are given data on the hatchability secured from father-daughter outbred, father-daughter inbred, and control matings

Table 22. Per Cent Hatchability of Father-Daughter Outbred, Father-Daughter Inbred, and Control Matings

(British Ministry of Agriculture and Fisheries, 1934)

Breed	Father-Daughter Outbred and Control Matings			Father-Daughter Inbred and Control Matings		
	Period	F. D. O.	Control	Period	F. D. I.	Control
White Wyandotte.....	1927–31	55.2	64.6	1927–31	44.1	62.7
Rhode Island Red.....	1927–28	48.5	52.9	1927–29	51.1	63.6
White Leghorn.....	1927–28	48.9	81.4	1927–29	52.0	74.8

in White Wyandottes, Rhode Island Reds, and White Leghorns. The first two matings are forms of inbreeding. For the first form of inbreeding a cockerel was mated to unrelated pullets, and the next year the same male was mated to his female progeny secured from the first mating. This constitutes the father-daughter outbred mating. For the second form of inbreeding a family from the original outbred mating was selected, a cockerel of this family was mated to his sisters, and the next year he was mated to his female progeny secured from the brother-sister mating. This constitutes the father-daughter inbred mating.

The data in Table 22 show that in every case the hatchability in both forms of inbreeding was lower than that of control matings, in some cases the differences being very pronounced.

Hatchability often decreases as the intensity of inbreeding increases. The coefficient of inbreeding is a measure of the intensity of inbreeding and is expressed in terms of a percentage. The coefficient of inbreeding of a half-brother-sister mating is 12.50; of a full-brother-sister mating, 25.00; and of three generations of brother-sister matings, 50.00. Where less intense inbreeding is practiced, the coefficient of inbreeding, of course, is lower. The data in Table 23 show that in three different breeds hatchability decreased as the coefficient of inbreeding increased.

In spite of the fact that practically all the results of experiments

TABLE 23. HATCHABILITY IN RELATION TO COEFFICIENTS OF INBREEDING
(Jull, 1929, *J*; and Warren, 1934, *W*)

Coefficient of Inbreeding	Percentage of Hatchability, *J*		White Leghorns, *W*		Rhode Island Reds, *W*	
	Barred Plymouth Rocks	White Leghorns	Range in Coefficient of Inbreeding	Per Cent Hatchability	Range in Coefficient of Inbreeding	Per Cent Hatchability
12.50	47.3	58.4	0 to 10	71.9	1 to 10	56.0
25.00	40.1	56.6	11 to 20	66.1	11 to 40	54.0
37.50	21.0	52.0	21 to 50	61.6		
50.00		43.4				

on close inbreeding have demonstrated that hatchability tends to decline, the severity of the decline increasing as close inbreeding is continued, it should be noted that it was not inbreeding of itself that produced the deleterious results. The decrease in hatchability results from the segregation of deleterious genes present in the foundation stock used in inbreeding experiments. These deleterious genes tend to be brought together through inbreeding so that the hatching quality of the eggs is lowered and embryonic development cannot proceed normally. If the foundation stock is relatively free of deleterious genes and if rigid selection for high hatchability is practiced, it should be possible to maintain a relatively high level of hatchability.

Waters (1932) and Waters and Lambert (1936*a*, 1936*b*) practiced rigid selection for high hatchability among inbred families of White Leghorns for ten years and succeeded in maintaining a relatively high level of hatchability. In some instances, entire families were excluded from the breeding pens because of unsatisfactory results in hatchability. For the most part, the degree of inbreeding in each generation was less intense than in the case of brother-sister and parent-offspring matings although good hatchability was obtained from the eggs of birds with a coefficient of inbreeding as much as 80 per cent. The results are shown graphically in Fig. 41.

The deleterious effects of inbreeding on hatchability that usually result are shown to be due largely to increased embryonic mortality during the first four and especially the last three days of incubation. Payne (1919–20) observed a distinct early and a still more pro-

nounced late peak of embryonic mortality in the case of noninbred birds. Bronkhorst (1933), Byerly, Knox, and Jull (1934), and others made similar observations, the general conclusion being that the early peak of embryonic mortality occurs on the third day of incubation and the late peak during the last three days of the incubation period.

Bronkhorst (1933) compared the trend of embryonic mortality among two White Leghorn groups, one of which was comprised of individuals whose hatchability was below 50 per cent and the other of individuals whose hatchability was above 75 per cent. In the low-hatchability group, embryonic mortality amounted to 63.13 per cent of 857 fertile eggs, whereas in the high-hatchability group embryonic mortality amounted to 19.39 per cent. The great difference in the

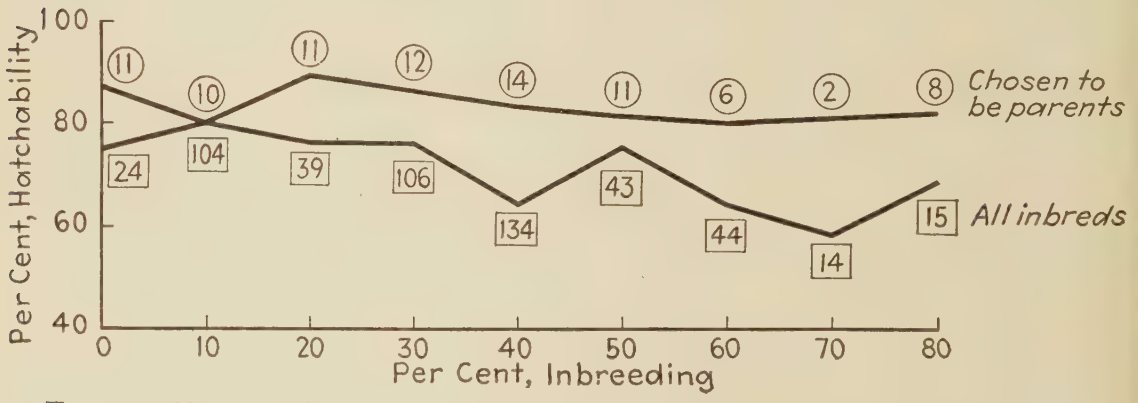

FIG. 41. Showing the trend in the average percentage of fertile eggs hatched for all inbreds and for those inbreds chosen to be parents, together with the number of birds in each group. (Waters and Lambert, 1936.)

embryonic mortality between these two groups suggests that many genes are involved in determining hatchability.

Byerly, Knox, and Jull (1934) compared the trends in mortality among embryos from an inbred strain of White Leghorns, which was comprised of 11 noninbred pure breeds and 35 crossbred matings. The inbred White Leghorns had a hatchability of 45 per cent of 1,371 fertile eggs and the noninbred pure breeds a hatchability of 69 per cent of 19,547 fertile eggs. The mortality curves are shown in Fig. 42. The curve of embryonic mortality for the inbred strain of White Leghorns indicates slightly greater mortality during the first week and much greater mortality during the last week than in the case of the embryonic mortality of the noninbred pure breeds. The embryonic mortality of the noninbred pure breeds was slightly greater during these two periods than in the case of the embryonic mortality of the cross breeds.

Crossbreeding Effects on Hatchability. If close inbreeding, especially without particular attention to the selection of breeding

TABLE 24. EFFECTS OF CROSSBREEDING ON HATCHABILITY

(Warren, 1927, *A*; Byerly, Knox, and Jull, 1934, *B*; Funk, 1934, *C*; Warren, 1934, *D*; and Knox, 1939, *E*)

Investigator	Kind of Mating	Per Cent Hatchability
A	White Leghorn purebred matings	73.0
	Jersey Black Giant purebred matings	57.0
	White Leghorns × Jersey Black Giants	78.0
B	11 purebred matings	69.0
	35 crossbred matings	76.0
C	Barred Plymouth Rock males × Barred Plymouth Rock females	57.0
	Rhode Island Red males × same Barred Plymouth Rock females	74.0
	White Leghorn males × White Leghorn females	70.6
	White Plymouth Rock males × same White Leghorn females	80.1
D	White Leghorn males × White Leghorn females	61.0
	Barred Plymouth Rock males × same White Leghorn females	80.0
	White Leghorn males × White Leghorn females	71.0
	Barred Plymouth Rock males × same White Leghorn females	80.0
	White Leghorn males × White Leghorn females	84.0
	Barred Plymouth Rock males × same White Leghorn females	86.0
E	White Leghorn purebred matings	70.0
	Rhode Island Red purebred matings	68.1
	Light crosses[1]	74.5
	Heavy crosses[2]	74.6

[1] The light crosses involved matings of White Leghorn males to Rhode Island Red, Black Minorca, and White Plymouth Rock females, except for one crossbred mating of White Plymouth Rock males × White Leghorn females.

[2] The heavy crosses included progeny from reciprocal matings of Rhode Island Reds and Barred Plymouth Rocks, Rhode Island Red males mated to White Wyandotte females, and matings of F_1 males or females obtained from different crosses mated to purebred birds of a different breed from that used in the original cross used to produce the F_1 males and females.

stock on the basis of high hatchability, tends to reduce hatchability, it remains to be determined the extent to which crossbreeding tends to increase hatchability. Crossbreeding consists of the mating of the sex of one breed to the opposite sex of another breed. The data on the effects of crossbreeding on hatchability show rather pronounced effects depending upon the genetic constitution of the parents that are crossed.

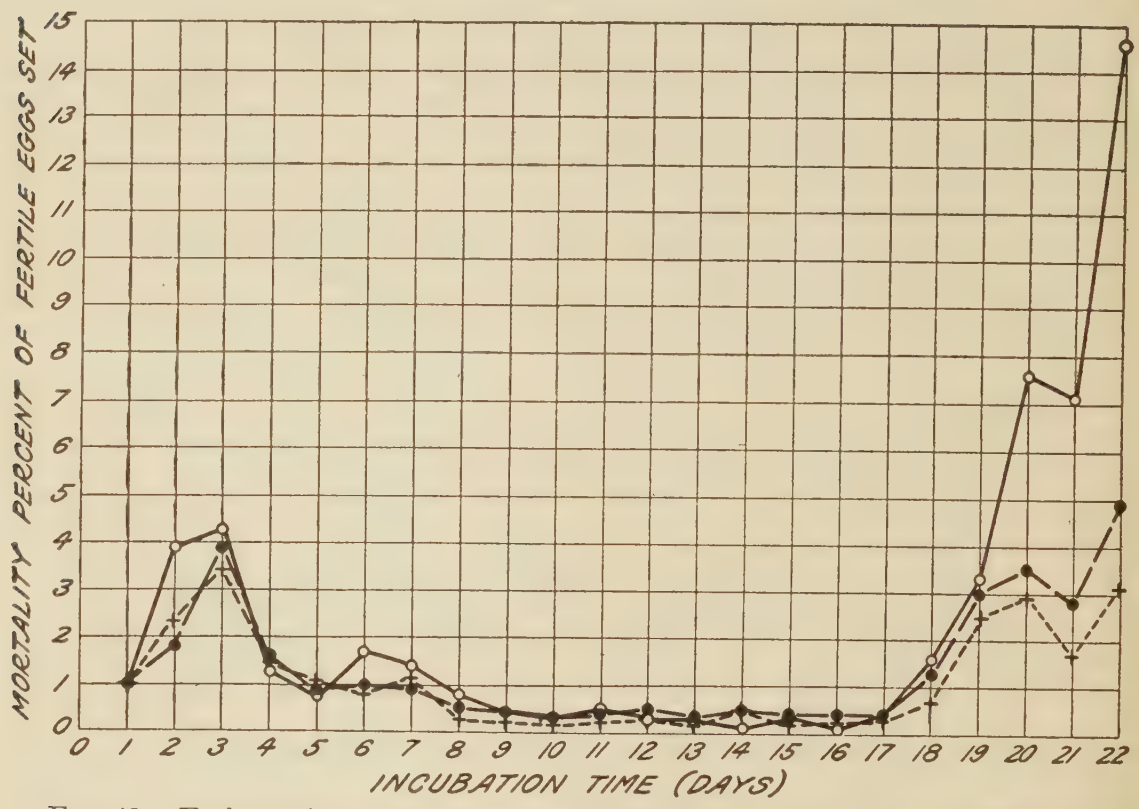

FIG. 42. Embryonic mortality in eggs from inbred Single Comb White Leghorns, ○; unweighted averages for pure breeds, ●; and unweighted averages for crosses between breeds, +. (Byerly, Knox, and Jull, 1934.)

The real purpose of crossbreeding is to provide for the combination of desirable qualities that already exist in two breeds. At the same time, it should be pointed out, as Jones (1925) has observed, that "Uniform progeny are produced only when the parental races are fixed in their particular type and breed true, and it is only when they are from separate and distinct lines of descent that decidedly beneficial results from crossing can be expected."

Pearl and Surface (1910) made reciprocal crosses between Barred Plymouth Rocks and Dark Cornish and found that the hatchability of the hybrid embryos was superior to the hatchability of the pure-bred embryos. The results of crossbreeding on hatchability secured by various workers are given in Table 24.

The results given in Table 24 show that crossbreeding tends to

increase hatchability. Byerly, Knox, and Jull (1934) point out, however, that the possibility of improving hatchability is limited, especially when both breeds that are crossed are noted for high hatchability. On the other hand, hatchability is likely to be improved materially when the hatchability of one or the other or both of the parental breeds is quite low.

Byerly, Knox, and Jull (1934) observed that during the first week of incubation, the mortality among crossbred embryos was practically the same as among purebred embryos, whereas during the last three days of the incubation period the mortality among crossbred embryos was slightly less than among the purebred embryos, as shown in Fig. 42. The increase in hatchability that results from crossing two breeds is said to be due to hybrid vigor or heterosis.

Increased hatchability has also been shown to result from the crossing of inbred lines by Dunn (1928), Hays (1929), Dumon (1930), Jull (1930), and Waters (1938). In Table 25 are given the results

TABLE 25. EFFECTS ON HATCHABILITY OF CROSSING INBRED STRAINS OF WHITE LEGHORNS

(Jull, 1930)

Strain	Percentage of Hatchability			
	Pen 1	Pen 2	Pen 3	Pen 4
Third-year inbred mating	55.7	49.9	55.8	33.7
Inbred matings intercrossed	57.4	57.5	62.7	50.0

secured by Jull (1930) from four pens of White Leghorns which had been inbred by brother × sister matings for three successive generations and then the pens were intercrossed. The third-year inbred male from Pen 1 was mated with the third-year inbred females of Pen 2, the third-year inbred male from Pen 2 was mated with the third-year inbred females of Pen 1, and in similar manner the third-year inbred males from Pens 3 and 4 were interchanged.

The data in Table 25 show that in every case hatchability was increased as the result of intercrossing highly inbred lines of White Leghorns. Waters (1938) secured similar results in mating highly inbred White Leghorn males that had been inbred for seven or more years, to noninbred White Leghorn females. Such matings have been called top-cross matings. Fig. 43 shows the differences in hatchability

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for each of five years among the top-cross, noninbred, and inbred matings.

Apparently the most plausible explanation to account for the increased hatchability resulting from crossbreeding is that complementary genes, including favorable dominant ones, are brought together by the two breeds. The crossbred embryos possess genes introduced by both parents of the cross and, therefore, are heterozygous for more genes, including favorable dominant ones, than either

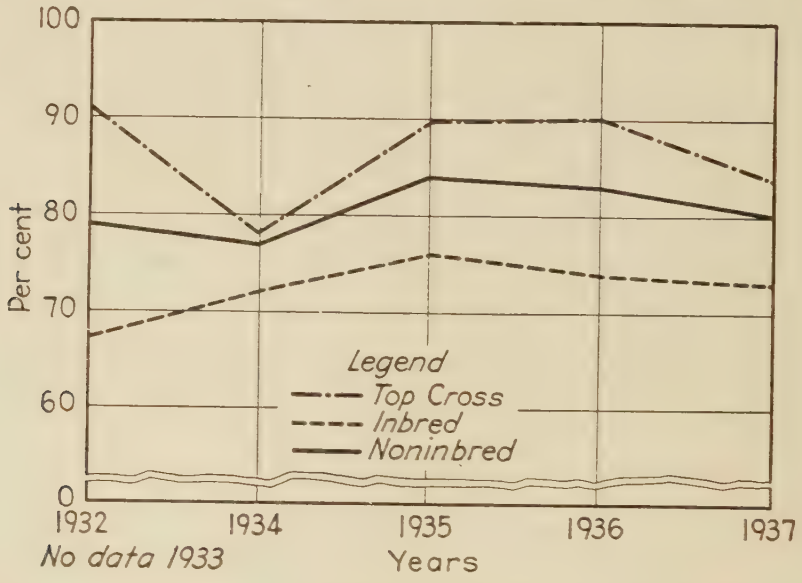

FIG. 43. Trends showing the percentage of fertile eggs hatched from hens in different groups. (Waters, 1938.)

of the parents. Since the embryos produced by the cross are heterozygous for more genes than are purebred embryos, and since dominant genes are frequently less deleterious than recessive ones, the heterozygous condition of the embryos from crosses gives rise to increased hatchability.

The favorable results secured from crossing highly inbred strains may be accounted for by the increased heterozygosity of desirable genes in the embryos produced by the cross, whereas the highly inbred embryos are homozygous for a relatively large number of undesirable genes. The crossing of highly inbred strains tends to recover some of the ill effects due to inbreeding.

Lethal Genes Lower Hatchability. During recent years it has been demonstrated that when certain matings are made, a particular gene from the sire and a similar gene from the dam brought together in the embryo cause its death. The lethal effect of the genes result from their being in a homozygous condition. Lethal genes are probably widespread among the various breeds of fowl, since at least seven have already been described.

The first lethal gene to be reported was by Dunn (1923*b*) from a cross between a Pit Game male and White Wyandotte females. Breeding tests showed that one of the White Wyandotte females carried a recessive lethal gene in a heterozygous condition and when she was backcrossed to one of her sons it was found that he also carried the recessive lethal gene in a heterozygous condition. This backcrossed mating produced 19 colored and 8 white breds, almost exactly a 2:1 ratio. The lethal effect of the recessive gene in a homozygous condition, being linked with the recessive gene for white, explains why one-half of the embryos that would normally develop into white birds die, giving a ratio of 2 colored birds to 1 white bird.

The lethal effect of another gene has been demonstrated by Landauer (1930) and Landauer and Dunn (1930*a*) in the case of the Creeper fowl, an outstanding characteristic of which is the shortness of its extremities. It was found that when Creeper birds were crossed with normal birds, the progeny were of the Creeper type, demonstrating that the gene responsible for the Creeper condition was dominant. It was further found that Creeper × Creeper matings always produced Creeper and normal progeny in the ratio of 2 Creepers to 1 normal instead of 3 Creepers to 1 normal. The Creepers that hatch are heterozygous for the Creeper gene. Data on different matings are given in Table 26.

TABLE 26. RESULTS SECURED FROM MATINGS OF CREEPER × NORMAL AND CREEPER × CREEPER

(Landauer, 1930 and 1937)

Mating	Progeny Secured		Progeny Expected	
	Creeper	Normal	Creeper	Normal
Creeper × normal	910	1,122	1,016	1,016
Creeper × Creeper, F_1	412	227	426	213
Creeper × Creeper, F_2	1,966	985	1,967.3	983.7
Creeper backcrossed to normals	486	477	481.5	481.5

The results given in Table 26 show that embryos possessing the Creeper gene in a homozygous condition fail to hatch. Not only do the F_1 results of Creeper × Creeper show that a ratio of 2 Creepers to 1 normal is secured instead of a ratio of 3 Creepers to 1 normal but the results of the F_2 generation also show that a ratio of 2 Creepers

to 1 normal is secured. The fact that when the dominant gene for the Creeper character is in a homozygous condition the embryo never hatches accounts for the ratio of 2 Creepers to 1 normal. Landauer (1932*a*) observed that most of the homozygous Creeper embryos die after three days of incubation and that as compared with normal embryos, the Creeper embryos are much retarded, especially in the region of the head and limb buds. Landauer (1933) furthermore observed that those homozygous Creeper embryos which continue development beyond the early critical stage show excessive abnormalities of the eyes, of the head generally, and especially of the extremities. In addition to the lethal effect of all homozygous embryos, there is also an increased embryonic mortality of embryos heterozygous for the Creeper gene. Landauer (1935*a*) has pointed out that unusual malformations occur sometimes in the Creeper stock which may involve heterozygous Creepers as well as genetically normal embryos.

Byerly and Jull (1930, 1932) reported a lethal mutation among the F_2 progeny of a mating between a Rhode Island Red male and Barred Plymouth Rock females. Abnormal embryos occurred which were reduced in size, had uncalcified bones, edema of varying extent, and unabsorbed allantoic and amniotic fluids. The results of various matings of birds heterozygous for the lethal gene included 169 abnormal or "sticky" embryos and 545 normal embryos, approximating a 3:1 ratio. Since the "sticky" embryos never hatch, it is apparent that the abnormalities observed are due to a recessive lethal mutation. Matings of normal males $\times$ heterozygous females resulted in a 71.5 per cent hatchability, whereas matings of heterozygous males $\times$ heterozygous females resulted in a 36.6 per cent hatchability. The gene for "stickiness" is lethal in a homozygous condition.

In the Cornish breed, Landauer (1935*b*) observed a recessive lethal mutation which is responsible for a shortening effect on the long bones of the extremities. Embryos homozygous for the gene die during the last few days of the incubation period or if alive at hatching time are unable to emerge from the shell.

Upp (1934) and Upp and Waters (1935) submitted evidence showing the existence of a sex-linked recessive lethal mutation in White Leghorn breeding stock.

Asmundson (1936) observed a recessive lethal mutation in an inbred strain of White Leghorns, the gene involved giving rise to deformed maxillae of the upper mandible. Hatching rarely occurs. The results of various matings show that the proportion of normal to affected embryos was close to a 3:1 ratio, 173 normal and 58 abnormal

embryos. The chief difficulty of embryos homozygous for the gene is their failure to hatch.

Hutt and Sturkie (1938) described the effects of a sex-linked recessive gene which is lethal to approximately half of the embryos during the last three days of incubation. The chicks that hatch are for the most part naked, as described in Chapter V, and mortality among them during the first six weeks is reported to be high.

Cole (1939) described the effects of a recessive autosomal lethal which had the effect of producing extreme polydactylism in the fore and hind limbs, which are frequently webbed so that the wing or foot appears to be palmated. Ectopia was reported to be present in all cases. The lethal character is recognizable at 110 hours of incubation by abnormalities in the development of the limb buds. In the majority of the cases, the gene in a homozygous condition is lethal at 6 to 8 days of incubation.

The presence of other lethal genes in poultry stocks has been reported by Serebrovsky and Petroff (1929) Gericke (1934), and Landauer (1938) and undoubtedly as time goes on other lethal genes will be reported.

On the other hand, there is some question concerning the extent to which lethal genes are responsible for any considerable portion of embryonic mortality in most of the flocks of the country. For instance, Byerly, Knox, and Jull (1934) have pointed out that every lethal gene that is transmitted must of necessity be carried by a bird in a heterozygous condition. Also, loss in hatchability resulting from a lethal mutation would probably be reduced to one per cent of otherwise hatchable eggs after only eight generations, provided no linkage existed between lethal genes and genes that determine desirable characters which may be perpetuated by proper methods of selection.

Many Genes Determine Hatchability. The various observations made in the preceding pages of this chapter show that hatchability is a very complex character determined by a large number of genes. Besides several genes that have a lethal effect, and probably many that are semilethal, there are genes that cause high early embryo mortality and other genes that cause high late embryo mortality as well as numerous other genes that exercise varying effects in determining degrees of hatchability among normal breeding birds.

THE INHERITANCE OF VIABILITY

Under the best of circumstances the span of life of the average chicken is relatively short so that frequent replacement is necessary. The average poultryman is obliged to replace approximately two-

thirds of his laying flock every year, but if his layers were profitable producers for several years, the annual cost of the replacement would be reduced considerably. During recent years, however, the trend of laying-pullet mortality has been definitely on the increase so that in many cases 50 per cent or more of the pullets that are placed in the laying house die before the end of their first laying year. Among the growing chicks raised each year, mortality is often excessive.

It has been shown previously that not only do a large number of genes determine the hatchability of eggs but that several different genes each produce specific effects on embryo mortality. On the other hand, it has been shown by Dunn (1921–22) and Jull (1928) that growing-chick mortality was not related to embryo mortality. It is apparent therefore, either that different genes are involved in determining embryo and chick mortality, or the genetic constitution of the organism causes it to respond differently under the conditions of incubation as compared with the conditions of rearing. As a matter of fact, the growing chick is subjected to many adverse environmental conditions, such as infections, diseases, and parasites, that are not encountered by the developing embryo.

Specific Genes Causing Chick Mortality. Just as there are specific genes that are lethal to embryos so there are other specific genes that are lethal to growing chicks. Knowlton (1929) described a condition in newly hatched chicks in which they are unable to stand, the head being drawn over the back with the beak pointing upward. They fall over and regain their feet only to repeat the performance. The condition was designated "congenital loco" and was found to be due to an autosomal recessive gene. Hutt and Child (1934) described an abnormal condition in some of the newly hatched chicks secured from a White Leghorn female mated to a closely related male and in other chicks secured from matings of related stock. Affected chicks exhibited varying degrees of tremor; some of them had their toes curled underneath and apparently partially paralyzed. It was this latter condition that led Hutt (1932) to designate the condition as "congenital palsy," but, since it was subsequently found that many of the chicks exhibiting the less extreme degree of tremor showed no signs of paralysis of the feet, Hutt and Child (1934) designated the condition as "congenital tremor." Most of the affected chicks died within a week after hatching, in many cases death resulting from inability to secure food and water. Chicks that survived the first month grew very slowly, only one female attaining sexual maturity. It has been suggested that the condition

is due to an autosomal gene "having an unusually low degree of penetrance because of the effects of modifying genes."

Age of Breeders and Viability of Progeny. Data on the influence of the age of breeding stock on the viability of growing chicks are of interest both from the biological and practical standpoints. Stewart and Atwood (1909) found that chicks secured from White Leghorn hens two and three years old had less mortality than chicks secured from pullets, whereas Pearl (1917) observed that in both male and female Barred Plymouth Rocks, the reproductive capacity was greatest in the first breeding year, as judged by the percentage of chicks alive at the end of the third week after hatching in proportion to the total number of eggs incubated.

Jull (1935) mated White Leghorn and Rhode Island Red males as cockerels and again as yearlings to yearling dams of their own breed and secured the results given in Table 27, the viability of the chicks being to four weeks of age and the viability of the pullets being from the time they were placed in the laying houses to the end of their first laying year, which was 365 days from the time that laying commenced in the case of each pullet. There was no culling of the pullets while in the laying houses.

The data given in Table 27 show that there was very little difference in the viability of chicks from the cockerel and yearling-sire matings but that in the majority of cases viability of laying pullets secured from yearling-sire matings exceeded that of pullets secured from cockerel-sire matings. At the same time, it should be pointed out that in no case is the difference significant.

In the United States, the great majority of the flocks that are used for breeding purposes consists of approximately two-thirds pullets and one-third yearlings and older birds. Specialty breeders who carry on pedigree breeding work use numerous matings consisting of yearling and older hens selected on the basis of their first-year performance. The relative merits of pullets and older birds as breeders from the standpoint of the viability of their progeny have been studied by a number of workers.

Based upon the results secured with Barred Plymouth Rock pullets and older birds, Pearl (1923) suggested the advisability of using as female breeders only the oldest hens in the flock with a view toward increasing longevity, or the average span of life, in the flock as a whole. It was also suggested that after about five years, the members of the flock would be noted for strong constitutional vigor and would produce chicks having extremely low mortality. Hays and Sanborn (1928), Kennard and Chamberlain (1934), Jull (1935), and Marble

TABLE 27. PERCENTAGE OF VIABILITY OF CHICKS AND LAYING PULLETS SECURED FROM YEARLING DAMS MATED TO WHITE LEGHORN AND RHODE ISLAND RED SIRES AS COCKERELS AND YEARLINGS

(Jull, 1935)

Breed	Sire No.	Percentage of Viability			
		Chicks to 4 Weeks of Age		Pullets, First Laying Year	
		Cockerel Sire	Yearling Sire	Cockerel Sire	Yearling Sire
White Leghorn	34	95.0	98.4	85.6	89.3
White Leghorn	41	95.7	95.6	76.9	84.1
White Leghorn	43	93.0	97.3	91.0	91.4
Rhode Island Red	127	88.6	88.1	80.0	90.0
Rhode Island Red	173	97.1	98.0	87.3	85.5
Rhode Island Red	330	88.9	95.1	94.5	93.6
Rhode Island Red	334	96.6	95.2	88.9	93.0
Rhode Island Red	338	97.9	98.5	90.2	95.4

(1939) have submitted evidence showing that, in general, the viability of the progeny of yearling dams exceeds the viability of the progeny of pullet dams. Comparable data are given in Table 28.

Hay's data are based on chick mortality to eight weeks of age and laying-pullet mortality during the first laying year. Jull's data are based on chick mortality to four weeks of age and laying-pullet mortality from the time the pullets were housed to the end of the first laying year, which was 365 days from the date of first egg in the case of each pullet. Marble's data are based on White Leghorn chick mortality to five weeks of age, Barred Plymouth Rock chick mortality to six weeks of age, White Leghorn laying-pullet mortality occurring from 151 to 515 days of age (365 days), Barred Plymouth Rock laying-pullet mortality occurring from 171 to 536 days of age (365 days).

Apparently, judging from the data in Table 28, chicks and laying pullets secured from yearling dams are slightly less liable to die than chicks and laying pullets secured from pullet dams. Yearling dams are shown to be superior as breeders when both chick and laying-pullet mortality is taken into consideration.

Jull (1935) compared the viability of chicks to four weeks of age

TABLE 28. VIABILITY OF CHICK AND LAYING-PULLET PROGENY OF PULLET AND YEARLING DAMS

(Hays and Sanborn, 1928, *H*; Jull, 1935, *J*; and Marble, 1939, *M*)

Breed	Year	Percentage of Viability			
		Chicks		Pullets	
		Pullet Dams	Yearling Dams	Pullet Dams	Yearling Dams
Rhode Island Reds, *H*	1923	94.4	91.6	75.0	72.9
	1924	88.9	93.9	43.0	50.0
	1925	77.3	88.2	73.7	77.0
	1926	81.2	91.1	69.8	68.0
White Leghorns, *J*	1925–1931	87.7	96.1	84.3	88.8
White Leghorns, *M*	1934	99.1	98.5	53.6	75.2
Barred Plymouth Rocks, *M*	1933	96.7	97.4	53.9	64.0
Barred Plymouth Rocks, *M*	1934	97.3	97.0	50.5	41.7

and of pullets during the first laying year among progenies secured from 55 White Leghorns and 51 Rhode Island Reds that were used first as yearlings and again as two-year-old birds, the results being given in Table 29.

TABLE 29. VIABILITY OF CHICK AND LAYING-PULLET PROGENY OF YEARLING AND TWO-YEAR-OLD DAMS

(Jull, 1935)

Breed	Percentage of Viability			
	Chicks		Pullets	
	Yearling Dams	Two-Year-Old Dams	Yearling Dams	Two-Year-Old Dams
White Leghorn	93.3	94.9	82.9	86.4
Barred Plymouth Rock	93.2	94.4	93.8	89.5

Judging from the data in Table 29 it would appear that the females used for breeding purposes as yearlings and as two-year-olds produced similar results so far as concerns the viability of their progeny.

Inbreeding Effects on Progeny Viability. The effects of inbreeding on the viability of chicks have been studied by Dunn (1923), Dumon (1930), and Dunkerly (1930), whose results are in substantial agreement in showing that close inbreeding has an unfavorable effect on chick viability. The results secured by Jull (1933) from four White Leghorn brother × sister matings for three years in succession show that such close inbreeding did not affect chick viability to four weeks of age to any marked extent except in the third year of inbreeding in two of the pens. On the other hand, there was greater viability of chicks in the F_3 generations in three of the pens than in the original matings.

In Table 30 data are given on the viability to sixteen weeks of age of chicks secured from father-daughter outbred, father-daughter in-

TABLE 30. VIABILITY TO SIXTEEN WEEKS OF AGE AMONG CHICKS SECURED FROM FATHER-DAUGHTER OUTBRED, FATHER-DAUGHTER INBRED, AND CONTROL MATINGS

(British Ministry of Agriculture and Fisheries, 1934)

Breed	Father-Daughter Outbred and Control Matings			Father-Daughter Inbred and Control Matings		
	Period	F. D. O.	Control	Period	F. D. I.	Control
White Wyandotte	1927–1931	63.0	78.0	1927–1931	65.1	76.4
Rhode Island Red	1927–1928	65.9	78.8	1927–1929	46.2	73.3
White Leghorn....	1927–1928	41.4	62.4	1927–1929	39.7	64.9

bred, and control matings. The first two matings are forms of inbreeding. For the first form of inbreeding, a cockerel was mated to unrelated pullets, and the next year the same male was mated to his female progeny secured from the first mating. This constitutes the father-daughter outbred mating. For the second form of inbreeding, a family from an original outbred mating was secured: a cockerel of this family was mated to his sisters, and the next year he was mated to his female progeny secured from the brother × sister mating. This constitutes the father-daughter inbred mating.

The data in Table 30 show that in every case chick viability was appreciably less under each form of inbreeding than under the control

matings. The results secured with respect to the viability of laying pullets from these two forms of inbreeding also showed that in general viability was less than in the control matings.

In their inbreeding experiments with White Leghorns, Waters and Lambert (1936) and Waters (1938) found that up to twenty-four weeks of age, there was no general decrease in chick viability as the inbreeding increased, except with respect to the viability up to eight weeks of age among chicks secured from birds having a coefficient of inbreeding of 80 per cent. On the other hand, it is stated that the viability of laying pullets decreased as the inbreeding increased, except with respect to the pullets secured from birds having a coefficient of inbreeding of 70 per cent. Practically all the pullets secured from the 80 per cent inbred birds died before the end of the first laying year.

Crossbreeding Effects on Progeny Viability. Although comparatively few well-controlled experiments have been conducted to determine the effects of crossbreeding on the viability of progeny, the results secured are of particular interest, especially to those interested in the production of broilers. Warren (1927) found that when White Leghorns were crossed with Jersey Black Giants the viability of the hybrid chicks to three weeks of age was superior to that of the White Leghorn and Jersey Black Giant purebred chicks. The viability percentages were as follows: White Leghorn chicks, 87.8; Jersey Black Giant, 80.1; hybrid chicks, 96.8. Warren (1930) also crossed White Leghorns and Rhode Island Reds and secured the results given in Table 31.

Table 31. Percentage of Viability of Chicks to Three Weeks of Age in White Leghorn, Rhode Island Red, and Crossbred Matings

(Warren, 1930)

Mating	Chick Viability
White Leghorn	94.0
Rhode Island Red	93.0
White Leghorn male × Rhode Island Red females	96.9
Rhode Island Red male × White Leghorn females	99.9

Knox (1937) observed that crossbred progeny obtained from several different crosses, on the average, had 13.3 per cent better viability than purebred progeny, viability being measured from hatching time to the end of the first laying year.

Dunn (1928) and Jull (1932) each crossed inbred strains of White

Leghorns and observed that the viability of the chicks of the crosse inbred lines exceeded that in the inbred lines before being crossed Waters (1938) crossed inbred White Leghorn sires with noninbre White Leghorn females and secured much better viability to twenty four weeks of age among the chicks of these matings than amon chicks of the noninbred and inbred matings.

TABLE 32. PERCENTAGE OF VIABILITY OF CHICKS TO TWENTY-FOUR WEEKS O AGE IN NONINBRED, INBRED, AND NONINBRED × INBRED MATINGS OF WHIT LEGHORNS

(Waters, 1938)

Year	Noninbred	Family	Inbred	Noninbred × Inbred
1932–1937	84.2	All families	77.0	89.7
		Family 1	71.0	90.8
1935–1937	83.6	Family 2	68.9	84.8
1935–1936	82.0	Family 3	63.4	84.9
		Family 4	72.7	96.1
1936–1937	84.6	Family 6	88.5	91.3
		Family 7	83.1	87.5

The data given in Table 32 show that the viability of the chick of the inbred matings was considerably lower than that of the non inbred matings but that the viability of the chicks of the noninbred × inbred matings was higher than the viability of chicks of the noninbred matings.

The crossing of highly inbred lines and the crossing of highly inbred and noninbred lines indicate that results are secured similar to those of crossbreeding, at least as far as the viability of chick progeny is concerned. The viability of chicks from crossbred matings is undoubtedly affected to a considerable extent by the vigor or by other qualities of the pure breeds that are crossed. Pure breeds in which the viability of chicks is high could not be expected to give materially higher viability when crossed, whereas pure breeds in which the viability is comparatively low would be expected to give considerably higher viability when crossed, as a result of the bringing together in the progeny of the favorable dominant genes from each of the pure-bred parents. The same principle apparently applies with respect to the crossing of highly inbred lines and the crossing of highly inbred and noninbred lines.

Genetic Resistance to Parasitic Infestation. Parasites in the form of large and small roundworms frequently invade the intestinal

tract of the chicken, the invasion frequently being so extensive as to result in retarded growth and even death. The resistance of chickens to the large roundworm *Ascaridia lineata* (Schneider) has been studied by Ackert (1935, 1939), who reported that Barred and White Plymouth Rocks and Rhode Island Reds were much more resistant to the roundworm than White Leghorns and White Minorcas. One strain of White Minorcas was found to be more resistant than another strain of the same variety. Differences in the genetic constitution of breeds and strains appear to have some influence in the ability to resist invasions of the large roundworm *Ascaridia lineata.*

Genetic Resistance to Disease. A few references are sufficient to demonstrate that breeds and different strains of the same breed differ in their inherent ability to resist a specific disease or abnormal condition.

From time to time observations have been made showing that breeds differ in their physiological response to unfavorable conditions. Hutt (1938) observed that White Leghorns were much more resistant to the fatal effects of extremely high temperatures than Barred Plymouth Rocks and Rhode Island Reds. Maximum temperatures of 101, 103, and 102°F. on three successive days resulted in mortality from heat of 1.8 per cent in White Leghorns, 5.2 per cent in Barred Plymouth Rocks, and 5.3 per cent in Rhode Island Reds. The suggestion was made that the genetic constitution of the White Leghorn enabled it to have more control over its thermoregulatory processes than was possible in the other breeds, differing as they do in certain genetic respects.

Further evidence of genetic difference between breeds with respect to their physiological response under certain conditions is revealed by the observations of Landauer (1937*a*, 1937*b*) on the metabolism of the Frizzle as compared with normal feathered chickens. The outstanding characteristic of the Frizzle breed is the curled condition of the feathers, which are brittle, thereby causing the body to become partly bare of feathers. The basal metabolism is much increased and other disturbances result, including the size and structure of the sex glands. Hatchability is reduced, chick mortality is increased, and sexual maturity is delayed.

Serfonteim and Payne (1934) observed that White Leghorns were more resistant than heavier breeds to a leg deformity known as "perosis" or slipped tendon. The distinctive symptom of perosis is a bowing or twisting of the legs, and the Achilles tendon slips out of its normal position and remains permanently dislocated.

The results of experiments conducted by Nichita and Iftimesco

(1934) and Nichita, Tuschak, and Calcef (1934) indicated that White Leghorns are relatively more resistant than Rhode Island Reds to a disease known as "polyneuritis," which is the result of a deficiency of vitamin B and is manifested in young and old birds by nervous disorders, culminating in the paralysis of the peripheral nerves. Lamoreux and Hutt (1937, 1939) confirmed the findings of Nichita and his co-workers and in addition showed that Barred Plymouth Rocks are also less resistant than White Leghorns to a deficiency of vitamin B.

Resistance to Bacillary Diphtheria. Probably one of the first reports on the mode of inheritance of the resistance to a specific disease was that of Frateur (1924). The results of experimental work with bacillary diphtheria led to the conclusion that resistance to this disease is due to a specific gene and that by proper selection the development of bacillary-diphtheria-resistant strains of poultry should be possible.

Resistance to Fowl Typhoid. Four generations of selection for resistance to a standard dose of fowl typhoid bacteria resulted in a decided decrease in mortality in the selected population of White Leghorns, according to an experiment conducted by Lambert and Knox (1928, 1932*a*, 1932*b*). Chicks hatched from the eggs of parents that survived an acute infection of fowl typhoid were found to be much more resistant to the disease than chicks from an unselected flock. Selection was furthermore found to be effective in increasing resistance to the disease through several generations.

Reciprocal crosses between selected and unselected birds demonstrated that resistance is transmitted by males as well as by females. The progenies of F_1, F_2, and backcross matings of birds from a parental cross of resistant $\times$ highly susceptible unselected birds indicated that resistance to fowl typhoid is genetic in nature, multiple genes being involved.

Resistance to Pullorum Disease. Regarding the inheritance of resistance to pullorum disease, Roberts and Card (1926) stated that on the basis of the results they had secured up to that time that resistance to the disease was hereditary. Chicks from certain hens were found to be much more resistant to infection than were chicks from other hens, and it was furthermore found that the occurrence of resistance was sufficiently consistent among chicks from certain hens and flocks to indicate that it should be possible to develop a strain of fowls highly resistant to infection with *Salmonella pullorum*, an organism which causes the disease.

Hutt (1935) showed that White Leghorns are more resistant to *Salmonella pullorum* than some of the heavier breeds. Roberts and

Card (1935), as the result of ten years of research on the inheritance of resistance to the pullorum disease, concluded that resistance was hereditary based upon the following facts:

1. Selection was found to be effective in producing strains more resistant than unselected strains.

2. Selected strains consistently maintained resistance through successive generations.

3. The F_1 generation produced by matings of resistant $\times$ susceptible was found to be as resistant as the resistant parents.

4. Progenies secured from matings of F_1 individuals $\times$ resistant individuals were significantly more resistant than were the progenies of backcross $\times$ susceptible.

5. In the F_2 generation, resistant and susceptible strains were recovered by selection.

6. The mating of susceptible male $\times$ susceptible females produced progeny that were much less resistant than were progenies produced by matings of susceptible male $\times$ resistant females.

7. The progenies of a resistant male mated to resistant and susceptible females showed no significant difference in the degree of resistance.

8. Since the progeny of infected hens exhibited no greater resistance than the progeny of noninfected hens, acquired immunity was not present in the experimental birds.

9. Resistance was observed to be dominant to susceptibility but that probably several genes are involved.

Hutt (1935) showed that lymphocytes in the blood were higher in White Leghorns than in Rhode Island Reds, pullorum infection usually being lower in White Leghorns than in Rhode Island Reds and similar breeds. Roberts, Severens, and Card (1939) reported that resistance and susceptibility to pullorum disease are related to the number of lymphocytes contained in the blood. The number of lymphocytes was greater in resistant than in susceptible strains. It was also found that when the number of lymphocytes in day-old chicks is reduced by X rays the degree of susceptibility is increased. It was concluded that the difference between resistant and susceptible individuals is due to an inherited differential in the number of lymphocytes at the time of greatest susceptibility to pullorum disease, which is immediately after hatching.

It is apparent that the inheritance of resistance to the pullorum disease involves numerous genes and that the selection of breeding stock with a view toward developing strains that are resistant to the disease is an extremely complicated problem.

Resistance to Fowl Paralysis. The results of research on the inheritance of fowl paralysis (a general term including leucosis, lymphocytosis, neurolymphomatosis, tumors, and related conditions) are of tremendous importance to the poultry industry in view of the appalling losses which the industry has suffered during recent years as the result of the ravages of the disease. Pappenheimer, Dunn, and Cone (1926) stated that their observations indicated a very significant breed or variety difference in susceptibility to paralysis, and Doyle (1926, 1928) secured evidence indicating that fowl paralysis is inherited. Asmundson and Biely (1932) furnished data indicating that resistant and susceptible birds differ by a single dominant gene, additional evidence in support of this theory being furnished by Biely, Palmer, Lerner, and Asmundson (1933). It should be noted, however, that in both of these experiments, the number of birds involved was rather small.

Kennard and Chamberlin (1934) observed that the flock with which they had been working for several years was more resistant than birds which were purchased as baby chicks from nonaffected flocks and reared with their own birds.

Gildow, Williams, and Lampman (1936) found that the disease developed less extensively among the progeny of affected parent stock than among the progeny of nonaffected parent stock. The progeny of certain individual hens were found to be more resistant than the progeny of other hens.

Upp and Tower (1936) observed inherent differences in resistance to fowl paralysis. Williams, Gildow, and Lampan (1938) observed a marked decrease in the incidence of the disease among chicks hatched from affected stock during a three-year period, the incidence of the disease for each of the three years being, respectively, 31.1, 19.9, and 6.9 per cent. On the other hand, the incidence of paralysis among chicks hatched from paralysis-free stock for each of the same three years was, respectively, 43.3, 41.6, and 41.8 per cent, thus showing a high degree of susceptibility upon exposure. Among chicks hatched from hens and pullets mated to males of similar ages and breeding, the incidence of paralysis among the pullet-hatched chicks was considerably greater than among the hen-hatched chicks. It was also found that there were marked differences in the incidence of the

disease among the progenies of different males as well as among the progenies of different females mated to the same male.

Wilcke, Lee, and Murray (1938) were able to develop by selection two groups of birds that proved to be significantly different with respect to the incidence of paralysis between their progenies. They found that hens mated to the same male differed greatly with respect to the incidence of the disease among their progenies and concluded that it should be possible to develop by selection, strains of birds possessing a relatively high degree of resistance.

Marble (1939) observed marked family differences in the extent to which resistance to fowl paralysis is developed by selection methods. Hutt, Bruckner, and Cole (1939) found that after three years of breeding to increase viability the incidence of mortality in a resistant strain decreased from 64.1 per cent to 50.3 per cent, whereas the incidence of mortality in a susceptible strain increased from 64.1 per cent to 69.0 per cent, the data including deaths occurring between 160 and 500 days of age. It was also found that among the birds that died, death occurred on the average seven weeks later in the resistant than in the susceptible strain. Birds belonging to the resistant strain outcrossed to males from another strain which had been bred for viability for a period of eight years, gave a second generation incidence of mortality of 44.1 per cent. It was found, as recorded by other workers, that the results secured from different females mated to the same male sometimes give widely different results. It was found, for instance, that one female had 17 daughters living at 160 days and only one died up to 500 days, whereas another female had 15 daughters living at 160 days but all died prior to 500 days. It should be kept in mind, of course, that not all the mortality that occurred in these strains and families was due to fowl paralysis, although it was the most important single disease causing mortality.

The results of the numerous experiments conducted on the resistance to fowl paralysis indicate that the problem is an extremely complicated one, which is quite understandable when it is realized that fowl paralysis is spread by contact of diseased birds with healthy ones. Moreover, it seems probable that numerous genes are involved in the inheritance of resistance to fowl paralysis, which in itself appears to be a complex disease.

The Genetics of Disease Resistance. From the time that Crew (1926) pointed out that immunity from disease is an hereditary character that can be developed by selection, a considerable amount of research has been undertaken to determine the physiological factors

involved in the inheritance of resistance to disease. In a very excellent paper on the inheritance of immunity among animals, Kozelka (1929) has observed that every infectious disease results from the struggle between the individual that is attacked and the pathogenic action of the microorganism. The final outcome of the struggle depends upon the vigor of the attack and of the counter attack, both of which vary according to the prevailing physical and physiological conditions, with environment also an important factor.

It is well recognized by practically all poultrymen that birds are in constant contact with microorganisms of virulence, indicating that many individuals are highly resistant to the invasions of the microorganisms. In a normal state of health, the chick and the laying hen possess a defensive mechanism which enables them to resist the attacks of the invading organisms with varying degrees of success. As long as the skin is not injured, it offers a considerable degree of resistance to organisms of various kinds. The lining membranes of the digestive tract also resist invasion with a considerable degree of success unless they are seriously injured by internal parasites or by faulty diets. The white blood corpuscles of the blood stream are able to destroy invading organisms by ingesting them. The blood serum contains certain protective substances called "antibodies," which are produced by an antitoxin reacting to the presence of the toxin carried by the invading organism. The last line of defense against invasion by organisms is natural resistance.

The results of research on the inheritance of resistance to specific poultry diseases leaves no doubt that resistance to a disease is inherited, in all probability in a Mendelian manner. However, since the degree of resistance varies with the prevailing physical and physiological conditions, it is quite apparent that the inheritance of susceptibility to an infectious disease is fairly complex.

Crew and Roberts (1933) have pointed out that, since practically all simply inherited conditions are rare, the great majority of affected individuals results from the mating of parents that are heterozygotes or carriers. Lambert (1935) has observed that from the results of research that has been conducted, the hereditary basis of resistance or susceptibility to infectious poultry diseases probably depends upon multiple genes. Gowen (1937) has suggested that the segregation of specific genes for resistance or susceptibility to disease initiated by pathogens may be responsible for immunity or mortality within the exposed population and that the segregation of genes for pathogenicity may make a pathogen virulent, mildly invasive, or innocuous.

INHERITANCE OF RATE OF FEATHER GROWTH

Throughout the lifetime of the chicken several changes in plumage take place, the down at hatching time being superseded by chick feathering, which is followed by juvenile plumage, which in turn is followed by adult plumage; finally, there is the annual molt. Chick feathering replaces the down gradually and subsequent feather changes result from the replacement of feathers in a fairly regular sequence from chick feathering to juvenile plumage and then to adult plumage.

Appearance of Chick Feathering. It has already been pointed out in Chapter II and illustrated in Fig. 37 that feathers arise from feather tracts, called "pterylae," the spaces between them being called "apteria." The flight feathers are termed "remiges" and the tail feathers are termed "rectrices." Jones (1907), in his study of the development of nestling feathers, concluded that the first down and successive feathers are developed from one continuous growth, a conclusion also reached by Rice, Nixon, and Rogers (1908). Observations on the appearance of definitive feathering in Barred Plymouth Rock chicks led Gericke and Platt (1932) to conclude that the order of the appearance of feathers in the ten different feather tracts was as follows:

Shoulder (humeral tract) Thigh (femoral tract)	second-third week
Rump (caudal tract) Breast (pectoral tract)	third-fourth week
Neck (cervical tract) Abdomen (ventral tract) Leg (crural tract)	fourth-fifth week
Back (dorsal tract)	fifth-sixth week
Wing coverts (alar tract) Head (caput tract)	sixth-seventh week

It is pointed out by Gericke and Platt, however, that the time of the appearance of definitive feathering in the tracts varied greatly. This is also borne out by the observations of Radi and Warren (1938), who have shown that in Rhode Island Reds and White Leghorns the order of the feather tracts from the standpoint of the first appearance of feathers is approximately as follows: shoulder, thigh, breast, neck, tail, back, web, leg, ventral, and head. Radi and Warren also

observed that chick feathering tends to appear somewhat earlier and is completed sooner in White Leghorns than in Rhode Island Reds.

In a detailed study of the appearance of definitive feathers in Brown Leghorn chicks, Chu (1938) has stated that by the second day after hatching seven or eight wing primaries and secondaries and their coverts had emerged and that on the third day some feathers appeared on the tail and shoulders. By the eighth day, new foci of feather growth were visible on the hallux and wing-bow area; by the thirteenth day, breast and thigh feathers began to emerge; by the fourteenth day, neck feathers appeared; by the fifteenth day, a row of minute feathers appeared on the frontal edge of the wing; by the seventeenth day, back feathers appeared; and by the twenty-first day, a line of feathers along either side of the sternum to the extreme posterior end of the body made their appearance. It is pointed out that up to this time, the number of feathers in the various tracts had increased rapidly and the chick plumage was complete.

Sequence of Plumages. Juvenile plumage succeeds the definitive feathering stage gradually, juvenile feathers making their first appearance in the marginal areas of the feather tracts.

The sequence of appearance and replacement of the juvenile plumage in birds has been studied by Heinroth (1898) and Dwight (1900), both of whom observed considerable variability in the sequence of molting. A detailed account of feather growth and replacement in Silver-Spangled Hamburgs has been given by Landauer and Dunn (1930), and in White Leghorns by Warren and Gordon (1931), who studied particularly the growth and molting of juvenile flight feathers.

Also in the case of White Leghorns, Marble (1934) observed two peaks of body molt between hatching time and twenty weeks of age and one complete wing- and tail-feather molt. Marble found that it was impossible to forecast age at sexual maturity in the females by the degree of primary wing feathering at eight weeks of age. Warren and Gordon (1935) extended their studies on the sequence of appearance and replacement of the juvenile flight feathers, including Light Brahmas and Rhode Island Reds, as well as White Leghorns. An irregular sequence of emergence and molt of the secondaries characterized all three breeds. During growth, one complete molt of the flight feathers usually took place and in some chickens, a second molt occurred as sexual maturity was approached.

Chu (1938) observed that it is only after the feather tracts are completely developed does molting and replacement of chick feathers take place. There is no sharp line of demarcation between the chick and subsequent feather types, for at the time of the completion of the

chick plumage there are still many follicles present which have not yet produced definitive feathers and the juvenile stage usually extends to more than one generation of feathers.

Chu points out that by six weeks of age juvenile feathers may be distinguished on the shoulder and wing-bow and that, when this has occurred, molting and replacement of chick feathers begin. "In this region, the replacement of feathers appears to be a random process, although, in most of the other parts of the body, it follows the order of feathering described for the chick." When the molting of the shoulder and wing-bow is completed, the molting of the rest of the chick feathers begins and follows the exact order in which they were laid down, the molt taking place very slowly and requiring a considerable period of time for its completion, with the result that a seriation of juvenile plumage types gradually approaching that of the adult is found. The juvenile plumage is not a discrete type but is regarded by Chu as a modified version of the adult form.

Feather Growth in Relation to Body Growth. Martin (1929) found that the rate of feathering over the back in Barred Plymouth Rocks was related to the rate of body growth, the faster growing birds usually being better feathered. Gerricke and Platt (1932) also found this to be true in their Barred Plymouth Rocks, high levels of protein in the diet inducing both faster body and feather growth than low levels of protein. Marble (1934) observed that in White Leghorns the faster growing birds, especially in the case of males, tended to be better feathered than the slower growing birds. The relationship between rate of body growth and rate of feathering was found to be at its maximum during the first few weeks. Schnetzler (1936) found that a relatively fast-growing strain of Barred Plymouth Rocks were much better feathered up to twelve weeks of age than a slow-growing strain selected from the same original stock.

Jaap and Morris (1937) made a study of the relationship between the degree of feathering and rate of body growth up to eight weeks in White Leghorns, Buff Orpingtons, White Wyandottes, Rhode Island Reds, White and Barred Plymouth Rocks, and reciprocal crosses between Buff Orpingtons and White Plymouth Rocks. By statistical analysis of their results, they concluded that approximately 50 per cent of the variation in feathering that occurs in a population is due to factors other than heredity. Hereditary variation in feathering is due to sex, dam, and sire, rated according to their relative influence. It was found that at eight weeks of age, the heavier birds tended to be better feathered than the slower growing birds. Radi and Warren (1938) found the same to be true in Rhode Island Reds.

Sexual Dimorphism in Rate of Feathering. Practically all the investigators who have studied feathering in growing chicks have observed that feathers appear earlier in females than in males. Reference has just been made of the fact that Jaap and Morris (1937) observed that sex was relatively more important than any other heritable factor in influencing rate of feathering. Radi and Warren (1938) showed that in females there was an earlier appearance of feathers in a given feather tract than in males and that a higher percentage of females than males exhibited feathering in a given

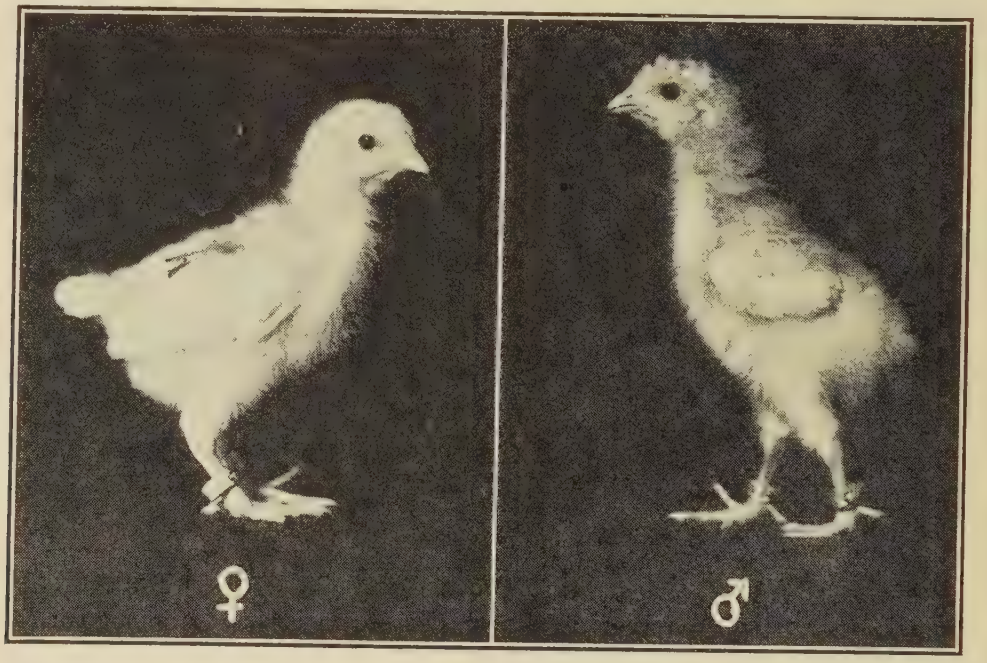

Fig. 44. Sex linkage of rate of feathering. Ten-day-old chicks from a mating of White Leghorn male × Jersey Black Giant female. The male chick has inherited the dominant sex-linked gene for slow wing and tail feathering from its dam. (U. S. D. A.)

feather tract at any period. Radi and Warren observed that in the female chick embryo the feather papillae appeared somewhat earlier than in the male chick embryo and that it was possible to distinguish the sex of the embryo by the relative development attained in its feather germs.

Sex-linked Rate of Feathering. It is a well-known fact that purebred Leghorn chicks acquire feathers somewhat earlier than purebred chicks of such breeds as Brahmas, Orpingtons, and Plymouth Rocks. Apparently, the first case of the sex-linkage of rate of feathering was that reported by Serebrovsky (1922) in a cross of Russian Orloffs × Barred Plymouth Rocks. Warren (1925) crossed White Leghorn males and Jersey Black Giants and observed that the sons were all of the slow-feathering type, whereas the daughters were of

the rapid-feathering type. In this mating, the Jersey Black Giant females transmitted slow feathering to their sons but not to their daughters. The reciprocal cross, Jersey Black Giant males × White Leghorn females, produced sons and daughters that were all slow feathering. The two matings demonstrate that slow rate of feathering is sex-linked and dominant to rapid rate of feathering.

Moreover, Warren (1925) found that when Leghorn males were mated to the first generation hybrid females obtained from a mating of Jersey Black Giant male × White Leghorn females, all the female

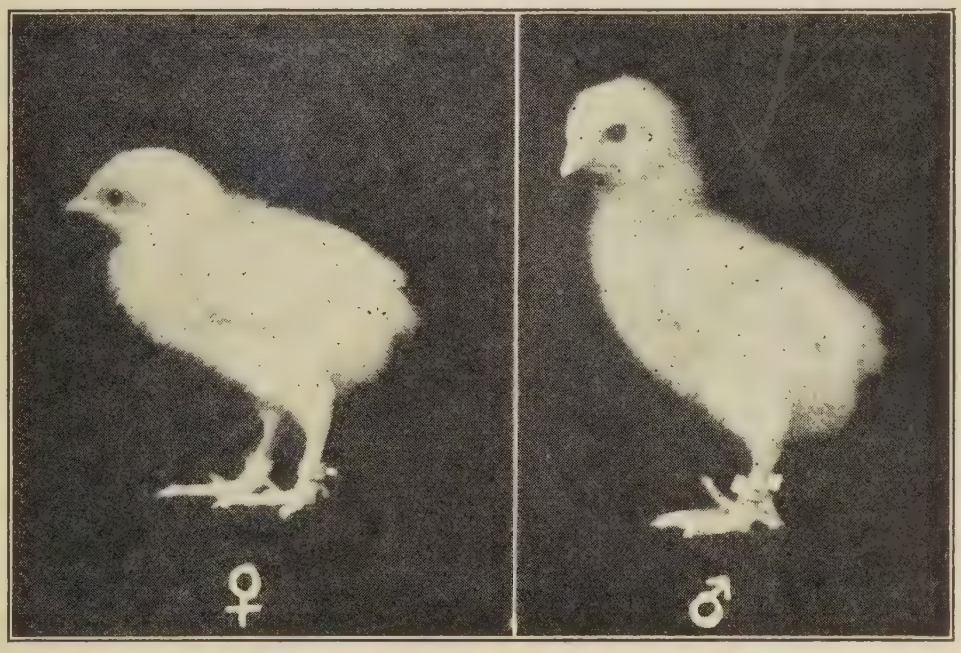

FIG. 45. Ten-day-old chicks from a mating of Jersey Black Giant male × White Leghorn female. Both sexes have inherited slow rate of wing and tail development from the sire. (U. S. D. A.)

progeny were rapid feathering and the male progeny were slow feathering. Such a mating is called a "backcross" mating: males that possess the recessive character in a homozygous condition (the male being homozygous for sex) are mated to females that possess the heterozygous dominant character (since the female is heterozygous for sex). Since from this backcross mating, only slow-feathering males and rapid-feathering females were secured, the results prove that slow rate of feathering is a sex-linked character.

Saharova (1926) crossed a Cochin male with Indian Pavloff females and observed that all the progeny were slow feathering, whereas an Indian Pavloff male mated to Cochin females produced slow-feathering cockerels and rapid-feathering pullets.

Kinugawa (1927) found that the male progeny were invariably slow feathering and the female progeny rapid feathering when White

Leghorn males were mated to females of the following varieties: Black Orpington, Barred Plymouth Rock, White Wyandotte, Rhode Island Red, Light Brahma, and Nagoya. He also found that the same results were obtained when Mottled Ancona males were mated to Rhode Island Red females and when Silver-Spangled Hamburg males were mated to Black Orpington females. The fact that rate of feathering is inherited as a sex-linked character has also been demonstrated by Horn (1927).

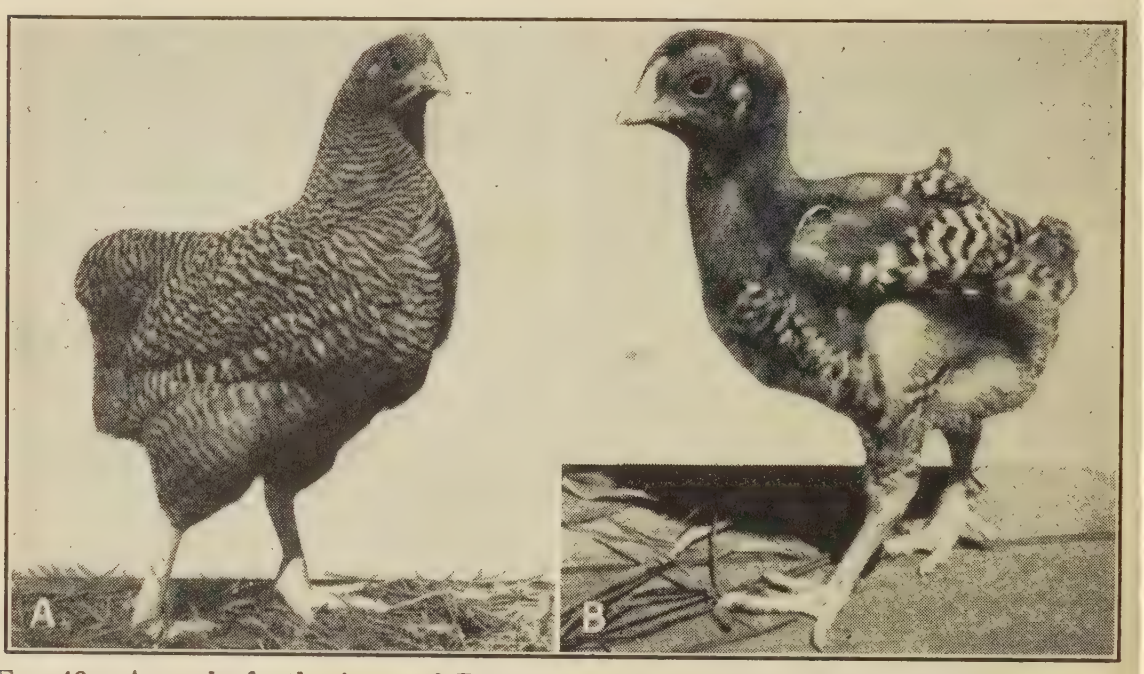

FIG. 46. A, early-feathering and B, late-feathering Barred Plymouth cockerels at 6 weeks of age. (Lloyd, 1939.)

Warren (1930*a*) points out that, from crosses involving the use of males possessing the gene for rapid feathering and females possessing the gene for slow feathering, the sex may be identified accurately by the extent of the growth of the primary and secondary wing feathers at hatching time and by the presence or absence of tail feathers at ten days of age. At hatching time, the primary or flight feathers in female chicks from a cross such as that between White Leghorn males $\times$ Rhode Island Red females are much more developed than those of male chicks obtained from the same cross.

Radi and Warren (1938) have demonstrated in Rhode Island Reds that it is possible to develop strains of rapid-feathering birds by taking advantage of the variability in rate of feathering that normally exists in this breed. Selection carried on for four years was effective in establishing a rapid-feathering strain that differed genetically from the normally slow-feathering strain, the degree of feathering being measured at seven weeks of age. A late-feathering strain of White Leghorns

was established by first making a cross of White Leghorn × Barred Plymouth Rock and then making several backcross matings to White Leghorns.

Warren (1933) found that some of his White Leghorns carried an autosomal recessive gene whose effect was exhibited in day-old chicks by a retarded development of all except the first three secondary flight feathers. In ten-day-old chicks, the gene has the effect of preventing tail development. The effects of the gene are expressed in the juvenile plumage only.

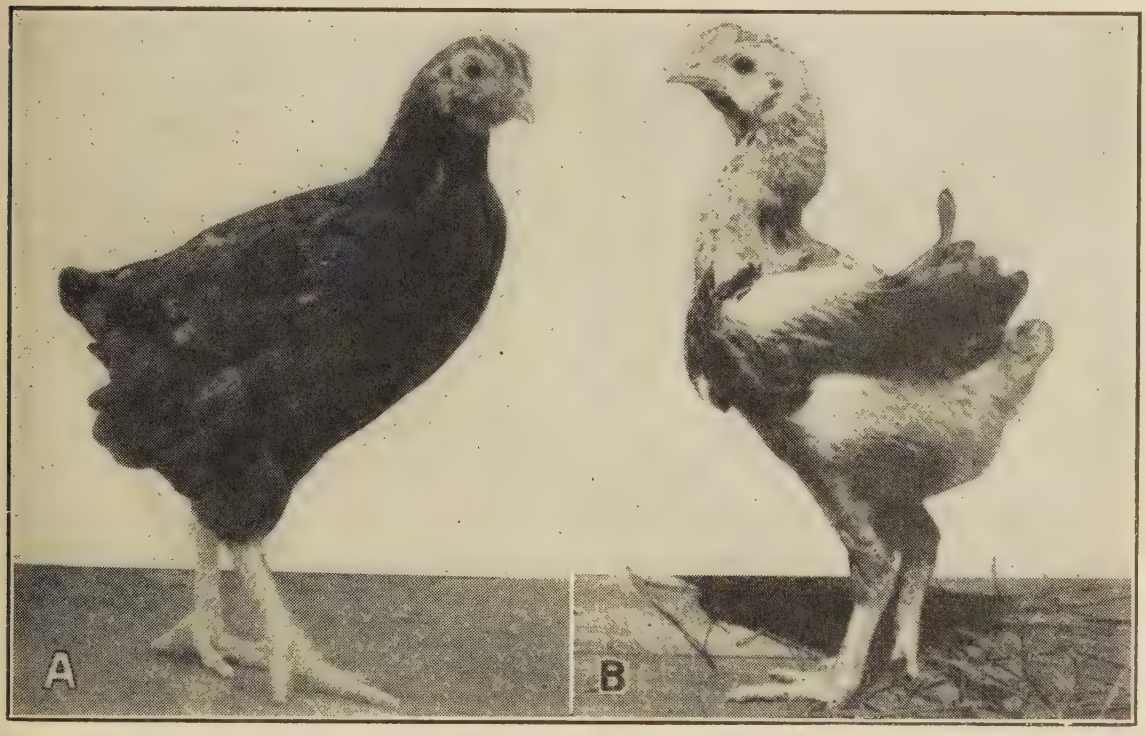

FIG. 47. A, early-feathering and B, late-feathering Rhode Island Red cockerels at 6 weeks of age. (Lloyd, 1939.)

INHERITANCE OF RATE OF BODY GROWTH

Aside from the fact that the males in each breed usually grow faster than the females and that birds belonging to the light-weight breeds, such as Leghorns and Anconas, reach body maturity earlier in life than heavy-weight breeds, such as Brahmas, and Plymouth Rocks, comparatively little evidence has been obtained on the inheritance of the rate of body growth.

Chick Weight at Hatching Time. Factors having possible genetic significance that might be thought to have some influence on the weight of chicks at hatching time have been considered by a number of investigators. Halbersleben and Mussehl (1922) found that chicks hatched from brown-shelled eggs were 64.9 per cent and those hatched from white-shelled eggs were 62.5 per cent of the original egg weight.

Jull and Quinn (1925*a*) found that, in Barred Plymouth Rocks and Rhode Island Reds, there is no significant difference in either sex in the percentage of chick weight to egg weight in yearling hen eggs as compared with pullet eggs. They found that the mean percentage of chick weight to egg weight was approximately 65.0 in the Barred Plymouth Rocks and approximately 66.0 in the Rhode Island Reds. Upp (1928) and Hays and Sanborn (1929), in the case of Rhode Island Reds, found that the percentage chick weight of egg weight was 68.0 and 61.0, respectively. Jull and Heywang (1930), in the case of White Leghorns, obtained a value 68.4 per cent.

Upp (1928), Hays, and Sanborn (1924), and Funk, Knandel, and Callenbach (1930) found that the rate of growth in chicks is not influenced by the weight of eggs from which the chicks were hatched.

Rate of Body Growth. Evidence showing that males grow faster than females has been submitted by Jull (1923) and subsequently confirmed by Ackerson and Mussehl (1930), Holmes, Pigott, and Campbell (1932), Kempster and Parker (1936) and others.

That differences exist between the rates of growth of certain breeds has been demonstrated by Card and Kirkpatrick (1918), Warren (1930), Waters (1931), Lerner and Asmundson (1932), Asmundson and Lerner (1934), Kempster and Parker (1936), and others. For instance, it has been demonstrated that Light Brahmas, Barred and White Plymouth Rocks, Rhode Island Reds, and Light Sussex grow faster during the first few weeks than White Leghorns and Anconas.

Asmundson and Lerner (1934) were led to conclude that the period from two to eight weeks is the most suitable one for a genetic study of differences in growth rates.

Although Asmundson and Lerner (1934) and Schnetzler (1936), among others, found that the growth rate to eight weeks of age was related to the final weight in Barred Plymouth Rocks and White Leghorns, Jaap and Morris (1937) found that their White Leghorns weighed slightly more than their Barred Plymouth Rocks at eight weeks of age. They concluded that growth to eight weeks of age is a separate entity not necessarily associated with mature body weight. Waters (1937) concluded that the rate of growth during the first few weeks has no bearing on the final body size attained but failed to determine the influence of time of hatch on rate of growth, which Kempster (1937) has shown to be quite important. Lerner and Asmundson (1938) have shown that the decreased early growth rate usually exhibited by chicks that were hatched late as compared with those hatched early leads to compensatory growth among the later-hatched chicks during the later growth stages. It was further observed

that differences in early growth rates between breeds reflected the differences in adult body size.

Data submitted by Kempster and Henderson (1923), Heuser and Andrews (1932), Kempster and Parker (1936), and others indicate quite clearly that strains of the same variety may differ widely in early as well as in late growth rates. The results conducted by different investigators are influenced not only by the genetic constitution of the strain but also by the methods of management and the kind of diet fed. The average adult size of strains of the same breed used by different investigators sometimes differed considerably.

Asmundson and Lerner (1933), on the basis of an analysis of the rates of growth from two to eight weeks among six families of White Leghorns, concluded that the six families could be divided into three classes from the standpoint of rate of growth: three families exhibited a relatively rapid rate of growth, two families exhibited an intermediate rate of growth, and one family exhibited a relatively slow rate of growth. It was concluded that genetic differences existed with respect to rates of growth within their strain of White Leghorns and that these differences in rates of growth are determined by multiple genes. This supports the previous evidence submitted by Lerner and Asmundson (1932) in their study on rates of growth in Light Sussex, Anconas, and progenies of reciprocal crosses between the two breeds.

Schnetzler (1936) demonstrated that three years of selection for rapid rate of growth and for slow rate of growth in Barred Plymouth Rocks resulted in a rapid-growing and a slow-growing strain with significant differences in rates of growth to twelve weeks of age.

Inbreeding Effects on Growth Rate. Very little research seems to have been conducted for the purpose of determining the effects of close inbreeding on growth rate. Waters and Lambert (1936), with White Leghorns and Knox, Quinn, and Godfrey (1939) with Rhode Island Reds and Light Sussex, secured results indicating that close inbreeding had no appreciable effect on rate of growth.

Crossbreeding Effects on Growth Rate. Since crossbreeding has become so widely practiced during recent years for the production of broilers, it is natural that a number of investigations should have been undertaken to determine the possible existence of differences between the rate of growth of hybrid progeny and the rate of growth of the purebred progeny of the parental breeds that are crossed.

Warren (1927, 1930*a*) and Waters (1931) observed that crossbred chicks weigh, on the average, the same as purebred chicks when the eggs from which they were hatched were of the same size. Shortly after hatching, however, there was an accelerated rate of growth in the

crossbred as compared with the purebred chicks. This accelerated rate of growth was maintained for approximately eight to twelve weeks, but at maturity the crossbred progeny were usually intermediate in weight between the weights of the purebred progeny.

Data on the weights of purebred and crossbred progeny at different ages reported by Warren (1930), Horlacher and Smith (1938), and Bice and Tower (1939) are given in Table 33.

TABLE 33. AVERAGE WEIGHT IN GRAMS OF PUREBRED AND CROSSBRED PROGENY AT DIFFERENT AGES

(Warren, 1930, *W*; Horlacher and Smith, 1938, *H*; Bice and Tower, 1939, *B*)

	Kind of Progeny	Weights in Grams at Specified Ages in Weeks						
		0	2	4	6	8	10	12
W	White Leghorn males	32	75	193	371	582	——	——
	Rhode Island Red males	34	79	204	413	670	——	——
	R. I. Red ♂ × W. Leghorn ♀, males	34	81	211	417	665	——	——
	W. Leghorn ♂ × R. I. Red ♀, males	34	85	220	431	685	——	——
	White Leghorn females	32	73	179	330	501	849	1099
	Rhode Island Red females	34	75	184	364	577	1008	1378
	R. I. Red ♂ × W. Leghorn ♀, females	34	74	184	356	548	944	1191
	W. Leghorn ♂ × R. I. Red ♀, females	34	81	202	378	592	1006	1296
H	Rhode Island Reds	36	86	178	328	538	768	1030
	White Wyandottes	38	84	201	380	652	917	1150
	White Plymouth Rocks	39	73	165	346	601	867	1083
	Barred Plymouth Rocks	38	83	192	338	570	785	990
	W. Wyandotte ♂ × R. I. Red ♀	36	94	230	409	707	1038	1363
	W. P. Rock ♂ × B. P. Rock ♀	37	90	194	361	612	871	1102
	W. P. Rock ♂ × W. Wyandotte ♀	37	82	182	342	583	819	1062
	W. Wyandotte ♂ × W. P. Rock ♀	38	84	189	373	643	884	1029
B	White Leghorns	37	99	227	391	584	——	——
	Barred Plymouth Rocks	37	105	238	368	612	——	——
	Rhode Island Reds	40	105	232	391	578	——	——
	Japanese Shamo Games	37	110	283	485	669	——	——
	J. S. Game ♂ × W. Leghorn ♀	37	113	278	470	660	——	——
	J. S. Game ♂ × B. P. Rock ♀	37	110	244	380	666	——	——
	J. S. Game ♂ × R. I. Red ♀	42	119	266	456	695	——	——

The Warren data in Table 33 show that crossbreeding provides a stimulus which accelerates growth during the first few weeks. The male progeny of White Leghorn dams mated to Rhode Island Red sires grew faster for eight weeks than the male progeny of White Leghorn dams mated to White Leghorn sires. Likewise, the male progeny of Rhode Island Red dams mated to White Leghorn sires grew faster than the purebred Rhode Island Red male progeny. It should also be noted that the male progeny of White Leghorn dams mated to Rhode Island Red sires grew faster than purebred Rhode Island Red males. The same trend is observable in the growth rates of the various female progenies, with two minor exceptions. During the 10–12-week period, the purebred Rhode Island Red females grew faster than the female progeny of Rhode Island Red dams mated to White Leghorn sires, and, during the 6–12-week period, the purebred Rhode Island Red females grew faster than the female progeny of White Leghorn dams mated to Rhode Island Red sires.

The Horlacher and Smith data given in Table 33 are for both sexes and reveal the effects of crossbreeding on early growth rate. The progeny of Rhode Island Red dams mated to White Wyandotte sires grew considerably faster for twelve weeks than the purebred Rhode Island Red progeny. The crossbred progeny of Barred Plymouth Rock dams grew faster than purebred Barred Plymouth Rock progeny and the crossbred progeny of White Plymouth Rock dams grew faster during the first ten weeks than purebred White Plymouth Rock progeny. It should be noted, however, that the purebred progeny of White Wyandotte dams grew faster than the crossbred progeny of White Wyandotte dams.

The Bice and Tower data given in Table 33 confirm the previous observations made concerning the stimulating effects of crossbreeding on early growth. The crossbred progeny of White Leghorn, Barred Plymouth Rock, and Rhode Island Red dams grows faster for eight weeks than the purebred progeny of the dams of these three breeds.

Further evidence concerning the effects of crossbreeding on early growth rates is provided in data supplied by Jaap and Morris (1937) and Knox (1939).

The data in Table 34 show clearly that crossbreeding tends to stimulate growth during the first eight or ten weeks. In every case, the crossbred progeny of the various dams weighed more than the purebred progeny of dams of the same breed.

The Genetics of Growth Rate. The previous discussion has shown clearly that rate of growth is a very complex phenomenon whose mode of inheritance has not yet been determined. At the same

TABLE 34. AVERAGE WEIGHT IN GRAMS OF PUREBRED AND CROSSBRED PROGENY AT SPECIFIED AGES

(Jaap and Morris, 1937, *J*; and Knox, 1939, *K*)

	Kind of Mating	Age in Weeks	Male Progeny	Female Progeny
J	White Plymouth Rock ♂ × White Plymouth Rock ♀	8	537	471
J	Buff Orpington ♂ × Buff Orpington ♀	8	598	556
J	White Plymouth Rock ♂ × Buff Orpington ♀	8	606	557
J	Buff Orpington ♂ × White Plymouth Rock ♀	8	640	563
K	White Wyandotte ♂ × White Wyandotte ♀	10	566	—
K	Light Sussex ♂ × Light Sussex ♀	10	602	—
K	Rhode Island Red ♂ × Rhode Island Red ♀	10	650	—
K	Rhode Island Red ♂ × Light Sussex ♀	10	690	—
K	Rhode Island Red ♂ × White Wyandotte ♀	10	642	—

time, it has been determined that rate of growth is inherited. Lerner and Asmundson (1938) have reported evidence of sex-linkage in growth rate in the Rhode Island Red × White Leghorn cross made by Warren (1930). Knox and Olsen (1938) and Knox, Quinn, and Godfrey (1939) obtained results from crosses between light-weight

TABLE 35. DOMINANT AND RECESSIVE PHYSIOLOGICAL CHARACTERS IN CHICKENS

Character	Dominant or Recessive	Autosomal or Sex-linked
Embryo lethal	Recessive, lethal when homozygous	Autosomal
Embryo lethal	Recessive, lethal in homozygous males and heterozygous females	Sex-linked
"Sticky" embryos	Recessive, lethal when homozygous	Autosomal
Creeper Condition	Dominant, lethal when homozygous	Autosomal
Cornish short leg	Recessive, lethal when homozygous	Autosomal
Deformed beak	Recessive, highly lethal when homozygous	Autosomal
"Naked" condition	Recessive, partially lethal during last 3 days of incubation	Sex-linked
Extreme polydactylism	Recessive, highly lethal when homozygous	Autosomal
Congenital loco	Recessive	Autosomal
Congenital tremor	Recessive	Autosomal
Hereditary blindness	Recessive	Autosomal
Slow feathering	Dominant to rapid feathering	Sex-linked

breeds and heavy-weight breeds that indicated sex-linkage for rate of growth. There are probably specific genes effecting early rate of growth and it is safe to conclude that many genes determine growth rate in general.

PROBLEMS

1. Is there any reason to believe that the average poultry breeder could develop a strain in which a hatchability of approximately 95 per cent could be maintained from year to year?

2. Account for the origin of lethal genes and mention at least six that affect hatchability.

3. Explain why inbreeding usually results in decreased hatchability and crossbreeding frequently results in increased hatchability.

4. Enumerate the more important factors to be kept in mind in developing a strain noted for laying-pullet viability.

5. Discuss the problem of the rate of growth in relation to standard body weights in the following breeds: Leghorn, Cornish, New Hampshire, Plymouth Rock, Orpington, and Jersey Black Giant.

6. Is it possible to combine standard quality of barring in Barred Plymouth Rocks with rapid growth and feathering?

7. How would you set about to develop a brown-egg, rapid-feathering strain?

8. Is there any particular relationship among the three following characters: hatchability, rate of growth, and laying-pullet viability?

9. What are some of the practical difficulties involved in breeding for resistance to a specific disease?

10. What are some of the more important characteristics that should be considered in selecting birds in the development of a strain for high hatchability, good viability of progeny, and rapid growth of progeny?

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CHAPTER VII

THE INHERITANCE OF EGG PRODUCTION

Egg production is of greater practical importance to poultrymen throughout all parts of the world than any other character which domestic fowls possess, and for that reason the discussion of the inheritance of egg-laying is given a separate chapter. A thorough study of the heredity of egg-laying characters includes the problem not only of the inheritance of egg-laying ability but also of the inheritance of the kind of eggs that are laid. In other words, consideration must be given not only to the number of eggs that are laid but also to their size, shape, color, and interior quality. In this chapter, the discussion is confined to the inheritance of egg-laying ability, the number of eggs laid per hen being the criterion; the discussion on the inheritance of egg characters is reserved for the next chapter.

The ability to lay eggs involves certain physiological processes, pertaining particularly to the formation of the egg, and certain genetic factors as a result of which there is variation among egg producers, thus making possible the development of highly productive strains through selection and the adoption of proper breeding practices. It follows, therefore, that due consideration must be given to the problem of the physiology of egg formation, discussed in Chapter II, before a complete understanding is possible concerning the problem of the genetics of egg production.

Moreover, the problem of the genetics of egg laying cannot be discussed without first determining the proper basis of comparing the inheritance of the egg-laying ability of any two hens. Egg production must be considered on a time basis, for the simple reason that a hen must lay a certain number of eggs in a given time in order to return a net income to her owner. The number of eggs that may be laid in any given time is affected by a variety of factors in addition to those of a genetic nature.

Effects of Domestication on Egg Production. The production of 300 or more eggs by the modern domestic fowl is something quite different from the production of some 12 to 30 eggs by the wild ancestor. Egg production sufficient for the reproduction of the species in the wild fowl has been developed in the domestic fowl into egg pro-

duction primarily for the purpose of supplying mankind with a highly important article of diet.

Whether or not the wild fowl would lay many eggs under modern methods of poultry keeping has apparently never been determined, but it is apparent that the onset of broodiness which naturally occurs after about 12 to 30 eggs have been laid is a factor determining the limited production. That the onset of broodiness may be retarded in wild birds is indicated from three citations by Pearl (1912*a*). Although the wild Mallard duck normally lays from 12 to 18 eggs, Austin (1908) observed that it will lay as many as from 80 to 100 eggs if each egg is removed from the nest daily and the duck is confined in a pen at night. Hanke (1908) by removing an egg daily from the common wryneck's nest, secured 48 eggs, and Wenzel (1908), using the same method with the house sparrow, secured 51 eggs.

Egg production among the descendants of *Gallus gallus domesticus* has undoubtedly been influenced by various management practices, including the providing of suitable shelter, the feeding of balanced diets, and the supplying of artificial illumination during the winter months in the northern hemisphere. Selection and the adoption of improved breeding methods have also played an important role.

Ways of Measuring Egg Production. A bird usually lays an egg a day for a few or a large number of days in succession and then misses one or more days, the number of eggs laid on consecutive days being called a "clutch." That the number of eggs laid in each clutch is a definite characteristic of each hen has been determined by Goodale (1918*a*), Hays and Sanborn (1927*a*), Atwood (1929), and Heywang (1938). The observations of Atwood and Heywang are particularly interesting inasmuch as they have shown that egg production follows a definite rhythm, the interval in hours between the laying of eggs on consecutive days depending upon the size of the clutch. The data in Table 36 show that the larger the clutch, the shorter the interval between layings.

The data in Table 36 show a regular trend of reduced time intervals between layings in a clutch as the clutch size increased. Heywang observed that the mean time interval between the laying of successive eggs in clutches of two, three, and four eggs was significantly greater in White Leghorn than in Rhode Island Red hens.

Heywang confirmed the observation of Atwood that the mean time interval between the last two eggs of a clutch is greater than the mean time interval between the first two successive eggs and that their mean time interval is longer than the mean time interval between successive

TABLE 36. MEAN INTERVAL IN HOURS BETWEEN LAYINGS OF SUCCESSIVE EGGS ACCORDING TO SIZE OF CLUTCH

(Atwood, 1929, *A*; Heywang, 1938, *H*)

Number of Eggs per Clutch	Mean Interval in Hours Between Layings		
	White Leghorns, *A*	White Leghorns, *H*	Rhode Island Reds, *A*
2	28.03	28.21	27.69
3	26.84	26.97	26.56
4	25.93	26.16	25.86
5	25.48	25.67	25.44
6	25.21	25.35	25.10
7	25.08	25.12	24.86
8	24.57	24.96	24.80
9	24.75	24.85	24.61
10	24.41	24.76	24.68
11	24.70	24.66	24.40

eggs laid near the middle of the clutch. A portion of the data submitted by Heywang is given in Table 37.

TABLE 37. MEAN INTERVAL IN HOURS BETWEEN LAYINGS OF SUCCESSIVE EGGS IN CLUTCHES OF DIFFERENT SIZES IN WHITE LEGHORNS

(Heywang, 1938)

Number of Eggs per Clutch	Nos. 1 & 2 Eggs	Nos. 2 & 3 Eggs	Nos. 3 & 4 Eggs	Nos. 4 & 5 Eggs	Nos. 5 & 6 Eggs	Nos. 6 & 7 Eggs
2	28.21					
3	26.57	27.37				
4	25.95	25.73	26.81			
5	25.72	25.14	25.27	26.55		
6	25.57	24.89	24.80	25.01	26.45	
7	25.59	24.89	24.43	24.69	24.99	26.34

The mean time interval between the first and second eggs in clutches of two, three, and four eggs was found to be significantly greater than the mean time interval between the first and second egg of any other clutch size. Also, the mean time interval between the first and second eggs in a clutch of five eggs was found to be significantly greater than the mean time interval between the first and

second egg of clutches of eleven or more eggs. The mean time interval between the second and third eggs in clutches of three and four eggs was found to be significantly greater than the mean time interval between the second and third eggs of longer clutches. On the other hand, there was no significant difference in the mean time interval between the second and third eggs of clutches of from six to twelve eggs and the mean time interval between the second and third eggs of longer clutches. Heywang pointed out that although the time sequence in the laying of successive eggs in clutches follows a regular trend, there were exceptions among birds that laid small-sized and large-sized clutches.

Warren and Scott (1935*b*) observed that in White Leghorns the average length of time between successive eggs was 25.1 hours and Scott and Warren (1936) observed that a break occurring in a clutch is due to delayed ovulation. Hens seldom ovulate in the afternoon and when laying occurs in the afternoon ovulation is delayed, a new clutch being initiated when laying occurs the morning following the day of nonlaying.

A number of interesting observations have been made concerning the relationship between intervals between eggs within clutches and annual egg production. Atwood (1929) found that the correlation between first-year egg production in White Leghorns and the mean time interval between layings within clutches during August was 0.41 ± 0.04, indicating that the shorter the interval between layings the greater the annual production. Hays (1936*c*) observed in Rhode Island Reds that the shortest time intervals between layings within clutches occurred during the month of April. It was also observed that short time intervals were associated with heavy laying and that short time intervals were characteristic of birds laying large-sized clutches. Hays (1938) found that short time intervals between clutches were associated with high winter production and high annual production.

A short period of egg production, which may include several clutches, followed by a nonproductive period has been termed a "litter" by Curtis (1914*a*) and others.

A "cycle" of egg production has been defined by Goodale (1918*a*) as a period of production alternating with a period either of decreased production or cessation of production, although during recent years, cycles of production have been considered from the seasonal standpoint, as, for instance, winter, spring, summer, and fall cycles. It should be observed at this time, however, that these so-called cycles of production are purely arbitrary designations and may have no

particular significance for the problem of the inheritance of egg production.

The most common way of measuring egg production has been the number of eggs produced in one year.

First-Year Production. The basis of determining the egg-laying ability of a bird has been the number of eggs laid during her first year of production. Frequently the first-year production has included the number of eggs laid from the first of October to the last of September; again, first-year production has included the number of eggs laid from the day of laying the first egg to 364 days thereafter. Both these methods of determining first-year production are somewhat arbitrary, the first being more arbitrary than the second.

It is true, of course, that birds entered in egg-laying contests must of necessity have an arbitrary time limit set for the beginning and end of the so-called year's production, for the simple reason that the contests must start and end on certain dates. On the other hand, a much sounder basis for determining first-year production, especially from the biological standpoint, is from the day of laying the first egg. It is possible, also from the biological standpoint, that the first-year production record should terminate when laying ceases just prior to the first annual molt. In studies on the inheritance of egg production, however, the usual method of determining first-year production has been from the day of laying the first egg to 364 days thereafter.

In a number of cases in the early studies on the inheritance of egg production it was customary to divide first-year egg production into four rather arbitrary periods, winter, spring, summer, and fall. Eggs laid during these periods were called "cycles of production." The interesting observations of Pearl (1911, 1912, 1914, 1915*a*, 1915*b*) and Pearl and Surface (1909*a*, 1909*b*, 1911) in their extensive analyses of egg-production records in Barred Plymouth Rocks at the Maine Experiment Station were largely responsible for the adoption of so-called "winter cycle" as a criterion of inherent laying capacity among birds. Prior to the time of their investigations it was rather unusual for birds in the United States to lay many eggs during the winter months, and, since they found that the best winter layers were usually the best annual layers also, they concluded that the winter cycle of production, from the first of November to the last of February, was of considerable significance in determining the inherent laying capacity of a bird.

However, after a comprehensive study of records of production in White Leghorns at the Utah Experiment Station, reported by Ball, Turpin, and Alder (1914) and by Ball, Alder, and Egbert (1916), Ball

and Alder (1917) were led to believe that the winter cycle does not represent correctly a biological entity. They also state that a record of production of three years is a safer guide than the record for the pullet year only in determining the inherent laying ability of a bird. Goodale (1918*a*) found no evidence of the existence of a winter cycle among Rhode Island Reds at the Massachusetts Experiment Station. Brody (1921), from an analysis of the first year of production of 4,210 Barred Plymouth Rocks at the Maine Agricultural Experiment Station and 1,000 White Leghorns in the Storrs egg-laying contests,

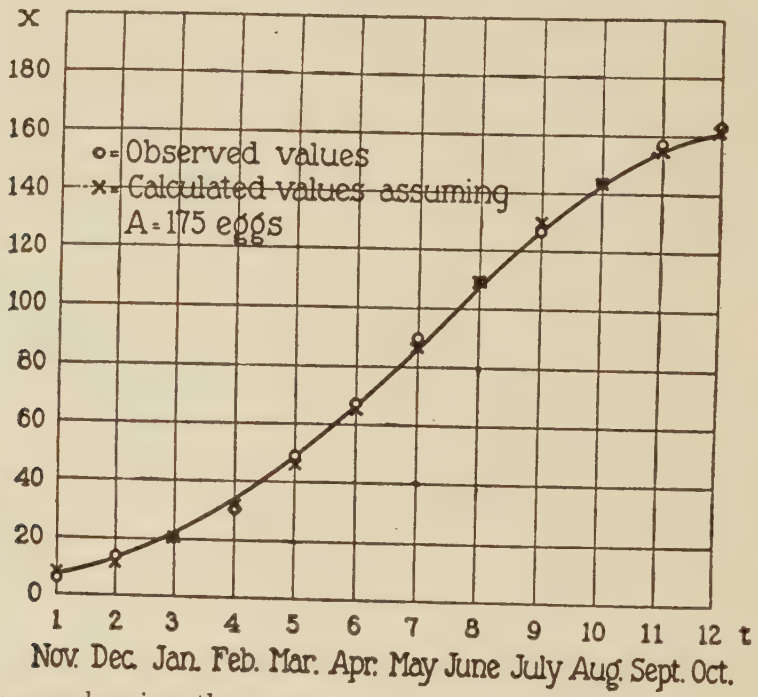

FIG. 48. Curve showing the average number of eggs laid by White Leghorns at the seventh Storrs international egg-laying contest. Ordinates represent the number of eggs laid (x) for the time (t); abscissæ represent the time (t) from November 1, the beginning of the observation, to any time of the year. (After Brody, 1921.)

found that the production of eggs is of the same general order as the growth of organisms, with no indication of the existence of cycles, as shown in Fig. 48. Harris and Lewis (1922*a*), from an analysis of records of production in White Leghorns, conclude that "there is no evidence of special factors which distinguish the 'winter cycle' from any other period of the year."

Harris and Lewis (1922*b*), in analyzing the first- and second-year records of production of 443 White Leghorns, found no evidence of special factors which distinguish the winter cycle of production from that of any other period of the year. Moreover, Harris, Kirkpatrick, Blakeslee, Warner, and Card (1921), from an analysis of the first-year production records of 1,840 Storrs-contest White Leghorns, and Harris,

Kirkpatrick, and Blakeslee (1921), from first-year records of 415 Storrs-contest White Leghorns, as well as Harris and Goodale (1922), from 1,658 first-year records made by Rhode Island Reds at the Massachusetts Experiment Station, have shown that the annual egg records of a series of birds may be predicted with a reasonable degree of accuracy when their production for a single month is known. They have also shown that a somewhat higher accuracy of prediction is possible when the production of two or more months is taken into consideration.

In a comprehensive statistical study of egg production of Wyandottes, Rhode Island Reds, Plymouth Rocks, and Leghorns entered in the Storrs egg-laying contests over a period of nine years, 1911–1918, Dunn (1924*a*, 1924*b*, 1924*c*, and 1927) found no evidence of cycles of egg production.

Criteria of Production. Trap-nesting a flock of layers throughout the first laying year is laborious, time-consuming, and expensive, but apparently is necessary as a part of the program of the pedigree poultry breeder who desires to secure detailed information concerning the periodical records of production made during the year. On the other hand, investigational work has demonstrated that it is possible to secure fairly reliable criteria of the total number of eggs laid during the first laying year without the necessity of trapping every day in the year. In fact, it has been demonstrated that relatively little trapping is necessary, if done at the right time. This should make it possible for a relatively large number of flock owners not at present engaged in trap-nesting, to determine approximately the laying ability of the members of their flocks. Granted that these flock owners trapping their birds at intervals were in a position to carry on pedigree breeding work, the benefits to the poultry industry might be very great.

It was found by Card (1925) that the total number of eggs laid on the first three days of each month was highly correlated with the number of eggs laid during the year. Voitellier (1930) found that the annual production of a bird could be predicted quite accurately by any one of the following three methods of recording the layings of each bird: (1) one day each week; (2) two consecutive days each week; (3) one week in every four weeks, the last method being the most reliable.

Dudley (1930–1931) found that the production records of one day each week or the production on four consecutive days in the middle of each lunar month served as a reliable index of annual production. Page (1931) observed that the records of production during any consecutive ninety-day period of the first five months of the laying

year served as a reliable index of first-year production. Thompson (1931, 1932) found that the number of eggs laid during October, November, and December served as a fairly reliable index of first-year production, but that when the number of eggs laid during the last thirty days of the first laying year were also added the index was much more reliable. Olsen (1939) found that among 500 White Leghorns and 300 Rhode Island Reds, trapping one day a week throughout the year measured the first-year production with an efficiency of 79.2 per cent in the Rhode Island Reds and 82.4 per cent in the White Leghorns.

It is quite obvious, therefore, that for all practical purposes, many flock owners could trap-nest their flocks one day a week throughout the year and secure sufficiently reliable information concerning the laying ability of birds to justify undertaking pedigree breeding work for the purpose of increasing the level of egg production in a flock.

Date of Hatch and Egg Production. In order to be able to compare the egg records of dams and daughters or of sisters, they should be hatched at relatively the same time each year because time of hatch influences egg production.

Goodale (1918*a*) has shown that Rhode Island Red pullets hatched at the Massachusetts Agricultural Experiment Station in March gave an average winter production of 42.65 eggs per bird, those hatched in April 35.40, and those hatched in May 22.50 eggs per bird. Card (1917) concluded that, in Connecticut, Leghorns should be hatched during late April or early May. Vickers and Cray (1925) report that in 150 farm flocks in Ohio the pullets which were hatched before the first of May laid an average of 152.9 eggs each, and those which were hatched after the first of May laid an average of 143.4 eggs each in their first year of production. Upp and Thompson (1927) shows that, in Oklahoma, pullets hatched not later than the first week in April lay much better during the first year of production than those hatched after the first week in April. Berry and Walker (1927) found that pullets hatched in April in New Mexico laid better than those hatched either in March or May or any other month of the year.

Knox (1932), in Iowa, studied the relationship between date of hatch and annual egg production in White Leghorns which were hatched from February 8 to June 8, inclusive, and found that the best egg production was obtained from the birds which were hatched from the latter part of March to the latter part of May.

At the same time, there are some commercial poultrymen who hatch their chicks during December and January in order that their pullets

may commence laying early enough to enable them to take advantage of the relatively high egg prices that usually prevail during the late summer and early fall. There are still other poultrymen who hatch chicks every month in the year.

Yearly Decline in Production. Brody, Henderson, and Kempster (1923) have shown that each year's egg production is 88 per cent of the preceding year's production. (See Fig. 49.) In other words, a first-year production of 200 eggs would be followed by a second-year production of 176 eggs, and a first-year production of 100 eggs would be followed by a second-year production of 88 eggs.

Hall and Marble (1931) have submitted data on the relationship between egg production in the first year and that of the second and later years in a large group of White Leghorns, records for three years being obtained from 1,867 birds and from fewer birds each successive year up to and including the eleventh year. The data are given in Table 38.

TABLE 38. ANNUAL EGG PRODUCTION IN SUCCESSIVE YEARS IN WHITE LEGHORNS AS A PERCENTAGE OF THE PRECEDING ANNUAL PRODUCTION

(Hall and Marble, 1931)

Year	Number of Birds	Mean Egg Production per Bird	Per Cent of First-Year Production	Per Cent of Preceding Year's Production
1	1,867	168.85	———	———
2	1,867	145.85	86.37	86.37
3	1,867	124.42	76.68	85.30
4	957	108.79	64.42	87.43
5	450	95.49	56.55	87.77
6	232	86.14	51.01	90.00
7	152	65.55	38.82	76.09
8	80	67.07	39.72	102.31
9	48	50.77	30.06	75.69
10	23	41.04	24.30	80.83
11	5	46.32	27.48	113.06

The data in Table 38 show that, in the same group of birds under observation for three years in succession, the second-year production was 86.37 per cent of the first-year production, and the third-year production was 85.30 per cent of the second-year production. These results are in close agreement with that secured by Brody, Henderson, and Kempster (1923).

On the other hand, Jull (1928) and Hall and Marble (1931) have shown that in Plymouth Rocks, Rhode Island Reds, and Wyandottes, egg production in the second year declines to a greater extent than in the White Leghorns of Hall and Marble. Moreover, Clark (1940) observed a decrease of approximately 19 per cent in second-year production under first-year production in White Leghorns, this being in agreement with the observation of Jull. It has been shown quite definitely that the higher the first-year production the greater the relative decline in second-year production.

The fact that in such varieties as Plymouth Rocks, Rhode Island Reds, and Wyandottes, second-year egg production as compared with first-year production declines to a greater extent than in White Leg-

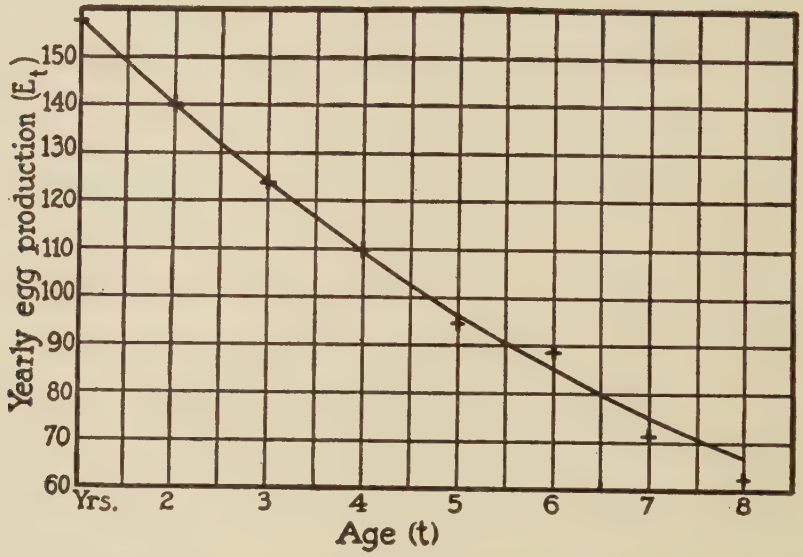

FIG. 49. The decline in egg production with age in the domestic fowl. The smooth line represents the computed values; the crosses represent the observed values. The values for the seventh and eighth years are not reliable due to the small number of individuals represented in the averages. (After Brody, Henderson, and Kempster, 1923.)

horns is made apparent from data submitted by Hall and Marble, as shown in Tables 38 and 39.

That there is a sensible relationship between second-year egg production and first-year egg production has been demonstrated by a number of workers, although the statements of Gowell (1903), Pearl and Surface (1909*b*), Ball, Turpin, and Alder (1914), and Ball, Alder, and Egbert (1916) were not in accord with this view. Nixon (1912) and Harris and Lewis (1922*b*, 1922*c*, 1923) show quite conclusively, however, that the best first-year layers were inclined to be the best second-year layers. In fact, Harris and Lewis concluded that those birds which are most persistent in laying at the close of the first year

TABLE 39. ANNUAL EGG PRODUCTION IN SUCCESSIVE YEARS IN BARRED PLYMOUTH ROCKS, RHODE ISLAND REDS, AND WYANDOTTES AS A PERCENTAGE OF THE PRECEDING ANNUAL PRODUCTION

(Hall and Marble, 1931)

Year	Number of Birds	Mean Egg Production per Bird	Per Cent of First-Year Production	Per Cent of Preceding Year's Production
1	372	191.60	———	———
2	372	137.91	71.97	71.97
3	132	109.72	57.27	79.56
4	42	91.36	47.68	83.27
5	14	84.86	44.29	92.89
6	7	63.57	33.18	74.91

are inclined to be the first in the resumption of laying in their second year.

To whatever extent the ability to lay well over a period of years can be developed in a flock by selection and breeding, to that extent the cost of reproducing the flock annually will be reduced. The

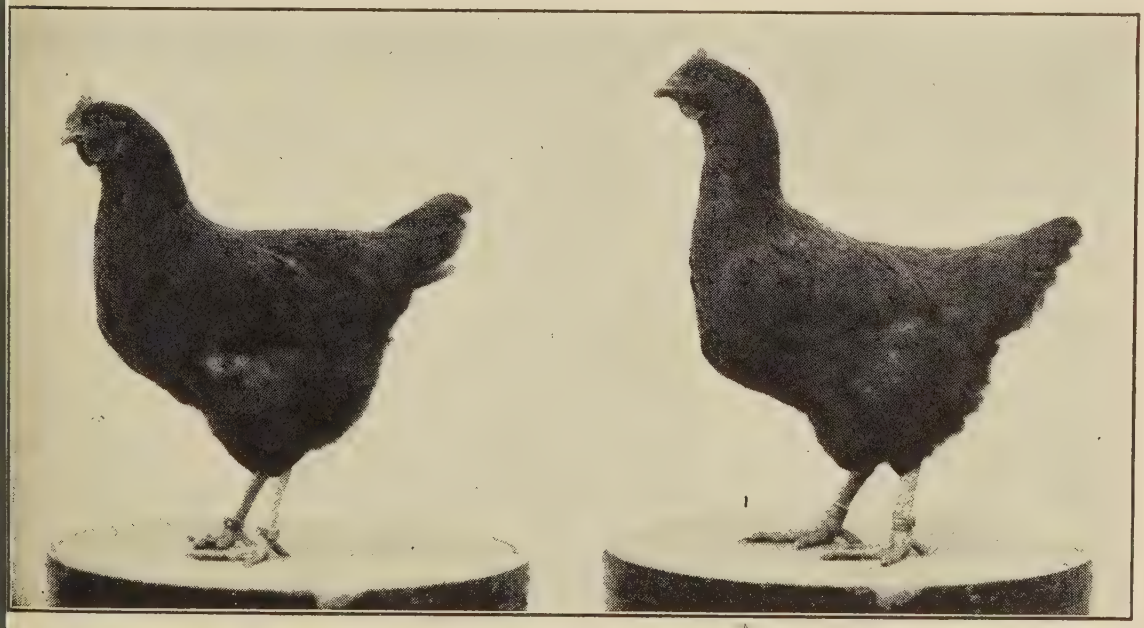

FIG. 50. Good egg production for several years is eminently desirable. The Rhode Island Red at the left laid 213, 206, and 203 eggs during her first, second, and third years, respectively. The Rhode Island Red at the right laid 260 and 207 during her first and second years, respectively. (Photo by U. S. D. A.)

inheritance of the ability to lay well over a period of years is of immense practical importance and is deserving of much more consideration than it has received up to the present.

THEORIES OF MENDELIAN INHERITANCE OF EGG PRODUCTION

The fact that egg-laying characters are inherited has been amply demonstrated by the results of investigational work and by the results which poultry breeders in all parts of the world have secured during the past quarter century. If it were not for the fact that egg-laying characters are inherited, it would hardly have been possible for practical breeders to develop flocks laying an average of 200 eggs or more per bird. When one realizes the vast difference in the average number of eggs laid by the wild fowl and the average production per bird of many modern flocks, the significance of the inheritance of egg-laying characters is fully appreciated.

Apparently the first piece of work attempted at a state institution to develop an egg-laying strain through the selection of female breeders based on trap-nest records was that of the Maine Agricultural Experiment Station with Barred Plymouth Rocks. The records of Gowell (1902, 1903) show that over a period of nine years, the practice of selecting female breeders according to their first-year trap-nest records failed to produce an increase in the average egg production per bird of the flock each succeeding year. The results secured were very disappointing at the time, for they seemed to demonstrate the apparent futility of improving egg production by selecting as breeders the best layers of the previous year.

The work of Gowell, however, laid the foundations for later work which was to demonstrate the value of the progeny test in breeding for increased egg production. Furthermore, the results which Gowell secured paved the way for the development of the three theories of the Mendelian inheritance of egg production which have been advanced. Continuing the breeding work with the Barred Plymouth Rocks at the Maine Agricultural Experiment Station, Pearl developed the theory of the sex-linked inheritance of so-called "winter egg production." Shortly thereafter, Goodale, working with Rhode Island Reds at the Massachusetts Agricultural Experiment Station, developed a different theory to account for the manner in which egg-laying characters are inherited. The Goodale theory was advanced further by Hays, who continued with the same flock of Rhode Island Reds. Shortly after Goodale's earlier publications dealing with the inheritance of egg production, Hurst developed his theory on the basis of the results which he reported that he had secured in White Leghorns and White Wyandottes.

The three theories of the Mendelian inheritance of egg-laying char-

acters differ in several details, although they are in agreement in pointing out that egg-laying is a complex character and that the selection of breeding stock based on the progeny test is the most practical way in which progress may be achieved in the development of high egg-laying strains. In the space available in this chapter, only the essential features of each of the three theories can be given.

The Pearl Theory. It has already been observed that Gowell failed to increase egg production in the flock of Barred Plymouth Rocks at the Maine station by the continued use of the highest producing dams. A different method of selecting the breeding stock in the same flock enabled Pearl to improve egg production to a considerable extent. An extensive series of papers by Pearl (1909*b*, 1911, 1912*a*, 1912*b*, 1914, 1915*a*, 1915*b*) deal with the results which he secured in numerous matings of Barred Plymouth Rocks and in crossbred matings of Barred Plymouth Rocks × Dark Cornish, the latter variety being regarded by Pearl as lacking the gene necessary for a winter production record of thirty or more eggs.

Using the so-called winter cycle, to March first, of the pullet year, as a basis for the analysis of records of production in Barred Plymouth Rocks, Pearl proposed a theory to explain the inheritance of winter production. The theory rested upon a sex-linked basis, two pairs of genes being involved, L_1 and l_1, being the dominant and recessive genes, respectively, of the pair located in one of the autosomes, and L_2 and l_2 being the dominant and recessive genes, respectively, of the pair located in the sex chromosome. Pearl postulated that, if a bird carried L_1 but not L_2, it would lay slightly less than 30 eggs up to March first, whereas, if a bird carried L_2 but not L_1, it would also lay less than 30 eggs up to March first, but that, if a bird carried both L_1 and L_2, it would lay more than 30 eggs up to March first. Since L_2 is sex-linked, it is apparent that dams could transmit it only to their sons, or as Pearl says, "high fecundity is not inherited by daughters from their dam."

It is not surprising that such an interesting theory of the Mendelian inheritance of winter egg production should stimulate further inquiry along similar lines, particularly since Pearl believed that his results applied to annual production as well as winter production. Goodale (1916, 1918*a*, 1918*b*, 1919), Goodale and MacMullen (1919), and Goodale and Sanborn (1922) in an analysis of the records of production in Rhode Island Reds at the Massachusetts station observed that Pearl's theory of the inheritance of fecundity is inadequate.

Moreover, in crosses involving the sex-linked genes for silver and barring, Punnett (1930) secured results that led him to conclude that

egg production is not sex-linked in its inheritance. Punnett mated an Indian Game male from a strain showing low fecundity to a White Wyandotte female that laid 240 eggs in her first laying year and came from a strain showing high fecundity. The F_1 males were all silver-barred, indicating that the White Wyandotte female carried both silver and barring.

An F_1 male was mated to Silkie females, showing low fecundity. The results secured indicate the absence of sex linkage in the inheritance of egg production. The mean egg production per bird of the 21 barred females was 123.7 eggs; for the 18 nonbarred females, it was 118.1 eggs; for the 28 silver females, it was 113.0 eggs; for the 11 gold females, it was 142.1 eggs. The number of birds in each of the four groups is rather small, but the results, taken together with other results secured by Punnett, do not seem to support the theory of the inheritance of egg production on a sex-linked basis.

A Light Sussex female that laid 200 eggs in her first year of laying was mated with the same Indian Game male which Punnett mated with the White Wyandotte female mentioned previously. The Light Sussex carries the sex-linked gene for silver, the female, of course, being heterozygous. The F_1 males carry silver, and one of them was mated to Silkie females. The results obtained show that the gold females laid somewhat better than the silver females, exactly opposite to expectation on the assumption of sex linkage for egg production.

The Hurst Theory. Although the Hurst theory of the inheritance of egg production was advanced after Goodale had put forth his theory, Hurst's theory is discussed first because it can be disposed of quite readily and because the observations made by Goodale have been added to from time to time up to the present by Hays.

Hurst (1921) apparently followed Goodale in regarding the annual egg production of a bird as being made up of several different characteristics. Hurst suggested five different heritable characteristics, to each of which he assigned a pair of autosomal genes that determine the number of eggs that a bird is capable of laying.

Early sexual maturity was regarded by Hurst as being dominant to late sexual maturity. Fast rate of winter production was regarded as being dominant to slow rate of winter production. Fast rate of spring production was regarded as being dominant to slow rate of spring production. Fast rate of autumn production was regarded as being recessive to slow rate of autumn production. Nonbroodiness was regarded as being recessive to broodiness. Maximum egg production would be possible when a bird contained the series of dominant genes in a homozygous condition and the two pairs of recessive genes in a homozygous condition.

The theory proposed by Hurst is quite interesting, but the evidence he supplied to substantiate his theory is wholly unconvincing to one fully appreciative of the complexities involved in determining the mode of inheritance of a quantitative character that involves various physiological processes.

Moreover, from evidence submitted in previous pages of this chapter, it appears quite certain that hens do not lay in so-called "cycles," as Hurst suggests. The various ratios which Hurst claims he secured are altogether too close to expectation to appear reliable. The observations made demonstrate the facility with which genes can be allocated to various birds in spite of insufficient evidence.

The Goodale-Hays Theory. The breeding of Rhode Island Reds at the Massachusetts Agricultural Experiment Station over a period of years enabled Goodale to accumulate a mass of data dealing with the inheritance of egg production. In one of his first papers, Goodale (1918*a*) reported that his results did not indicate that egg production was inherited on a sex-linked basis inasmuch as he found quite marked correlation between the egg production of dams and the egg production of their daughters. In another paper (1918*b*) he emphasized the complexity of laying performance as a hereditary character. Goodale and MacMullen (1919) and Goodale and Sanborn (1922) developed the conception that the first-year egg production of a bird is determined by five different characteristics: (1) age in days that laying commences, popularly referred to as sexual maturity; (2) intensity of production, popularly referred to as rate during a given period; (3) the amount of broodiness; (4) a so-called "winter pause" in production; (5) persistency of production, determined by the length of time that laying continues prior to the first complete annual molt. Goodale was led to believe that the same number of eggs might be produced by birds having different combinations of the five characteristics.

Breeding work with the Massachusetts station flock of Rhode Island Reds was continued by Hays, who has confirmed, for the most part, the observations of Goodale and has extended them into the most complete theory of the Mendelian inheritance of egg production that has yet been suggested.

In order that the reader may have a clear understanding of the theory developed by Hays and his co-workers, the complete theory is given here in comprehensive form, a discussion of various of its details being reserved for subsequent pages.

Genes for Earliness of Sexual Maturity. Hays (1924–1925) has suggested that the inheritance of earliness of sexual maturity, birds commencing to lay when less than 215 days of age, depends upon two pairs of genes, one pair of which is sex-linked. The dominant gene

of either of the two pairs of genes is capable of inducing earliness of maturity. The sex-linked genes are designated *EE* and the autosomal genes *E'E'*, the recessive genes in each case being *ee* and *e'e'*.

Genes for Rate of Laying. The inheritance of the intensity or rate of laying, rate being determined by the relative number of eggs laid from the time that laying commences to March first, has been reported to be determined by two pairs of autosomal genes designated *RR* and *R'R'*, the recessive allelomorphs being *rr* and *r'r'*. A production of over 50 per cent is attained when the two dominant genes *R* and *R'* are together in the same bird, the two genes being regarded as complementary to each other.

Genes for Broodiness. The inheritance of broodiness was studied by Goodale, Sanborn, and White (1920), who believed two pairs of complementary genes, *A* and *a* and *C* and *c*, to be involved. Broodiness is due to the presence of both dominant genes *A* and *C*, neither of which is sex-linked, according to Hays (1924–1925). Punnett and Bailey (1920) observe that more than one independent dominant gene could produce broodiness but believe that the genes involved are not complementary. Hays, however, has substantiated the views expressed by Goodale *et al.*, and Hays and Sanborn (1926, 1927*a*) point out that the degree of broodiness as well as the presence or absence of broodiness during the pullet year of production must be considered in the breeding program and that there is a somewhat higher winter intensity in broody than in nonbroody individuals. Hays and Sanborn (1927*b*) emphasize the importance of selecting as breeders nonbroody pullets that have a high winter intensity of production.

Gene for Winter Pause. Long, continuous records of egg production are the exception rather than the rule, even in strains that have been bred for egg production for several years. Broodiness naturally makes a break in the record of production, but, independent of this characteristic, Goodale (1918*c*) observed that many of his Rhode Island Reds exhibited a characteristic winter pause which lasted from a few days to as much as two months or more. Hays (1924–1925) found that the flock could be divided into two groups, those which exhibited a pause of one week or more and those which did not, and concluded that the winter pause is inherited and is due to the presence of a dominant autosomal gene *M*, from which it follows that birds showing a nonpause must be of the *mm* type, since the genes are borne in pairs. Hays and Sanborn (1927*b*) found no apparent association between winter pause and intensity.

Genes for Persistency. Hays and Sanborn (1927*b*) found a very intimate relationship between persistency of production and

annual production. High persistency of production is said to exist in birds that lay for 315 or more days prior to their first annual molt. Since persistency of production is so important, it is interesting to note that Hays (1927*b*) has suggested that high persistency is inherited in the ordinary Mendelian manner, the dominant gene *P* giving rise to persistency. Hays also points out that *P* is intimately associated with *E'*, previously described as the dominant nonsex-linked gene for early sexual maturity. It is apparent, therefore, that in order to develop a heavy laying strain, birds homozygous for *P* and for *E'* are necessary.

The fact should be appreciated, of course, that the Goodale-Hays theory of the Mendelian inheritance of the egg-laying characters is an attempt to interpret the results they secured in the breeding of their Rhode Island Reds. In this respect it is unfortunate that more concrete evidence has not been made available dealing with the inheritance of the five different characteristics which their theory recognizes as determining the number of eggs laid during the first laying year. One of the few papers containing ratios reported to have been secured from various matings is that of Hays (1924), but it is unfortunate that the number of progeny secured in most of the matings is quite small.

INHERITANCE STUDIES

Theories concerning the Mendelian inheritance of egg production are of little interest to poultrymen unless they can be applied in a practical way in the development of a profitable laying strain. Theories are of value, however, in presenting new points of view as well as in leading to an increase in existing knowledge.

The results secured by Pearl, Goodale, and Hays, and also those secured by Dryden (1921) demonstrate that, although the precise mode of inheritance of egg production has not been determined, egg production can be increased by adopting proper methods of selecting and mating breeding stock. Recent work has demonstrated the soundness of the suggestion originally developed by Goodale and Hays that the first-year egg production of a bird is influenced largely by at least the first, second, third, and fifth of the five following characters:

1. Age in days that laying commences, or sexual maturity.
2. Intensity of production, or rate of laying.
3. The amount of broodiness.
4. So-called "pauses" in production.
5. Persistency of production.

The importance, both absolutely and relatively, of each of these

characters is discussed and available information is presented concerning their mode of inheritance.

Inheritance of Sexual Maturity. By sexual maturity is meant the number of days between the date a pullet is hatched and the date she lays her first egg. From the purely practical standpoint, it is obvious, of course, that the earlier in life a pullet commences laying the sooner she begins to yield financial returns to her owner. In other words, a pullet that commences to lay early in life costs less to rear up to the revenue-producing stage than a late-maturing pullet. At the same time, the relative size of egg laid by the early-maturing and late-maturing pullet is of economic importance, as pointed out in the next chapter.

A number of investigators have shown that the time of the year that a pullet commences laying is important from the standpoint of the total number and value of eggs laid during the first laying year. Jull (1923) found that among 411 Barred Plymouth Rocks those commencing to lay in October laid more eggs per bird, and the eggs had a greater relative value, than those commencing to lay in September, November, and December. Kempster (1926) showed that among 1,110 White Leghorns those that commenced laying from October 16 to November 15 produced eggs having a greater value than birds that commenced laying either before or after these dates. Maw and Maw (1928) analyzed the egg-production records of 5,324 Barred Plymouth Rocks entered in the Canadian Record of Performance work and found that those birds which commenced to lay in September, October, and November laid approximately 180 eggs each, those in December approximately 168 eggs each, those in January approximately 154 eggs each, and those in February approximately 135 eggs each.

That it is possible to have birds in some flocks commence laying too early has been clearly demonstrated by the observations of Knox (1930*b*) in the first-year records of 684 Single-Comb White Leghorns. The results which Knox secured show that the birds that commenced laying in October laid the best, and that the birds that commenced laying in September, November, and December laid much better than those that commenced laying in July, August, and January. That birds commencing to lay as early as July or August did not make as good records as birds commencing to lay during the next four months was probably explainable by the fact that the birds that commenced laying during July or August underwent a partial molt during the fall and early winter, thus causing a break in their annual production.

Rice (1915) has shown that, in White Leghorn pullets, there is an

important relationship between earliness of sexual maturity and rate and persistency of production. Kempster (1925, 1926, 1927) reports that there is a significant negative correlation between sexual maturity and egg production for the first laying year. In other words, Kempster found that early-maturing pullets tend to make the highest annual records. Similar observations have been made by Ball and Alder (1917), Kennard (1921), Hervey (1923*a*, 1923*b*), Hays and Bennett (1923), Hays, Sanborn, and James (1924), Jull (1923*a*, 1924*b*), Parkhurst (1926), Knox (1927), Buster (1927), Hall (1934), Knox, Jull, and Quinn (1935), and Kimura (1937).

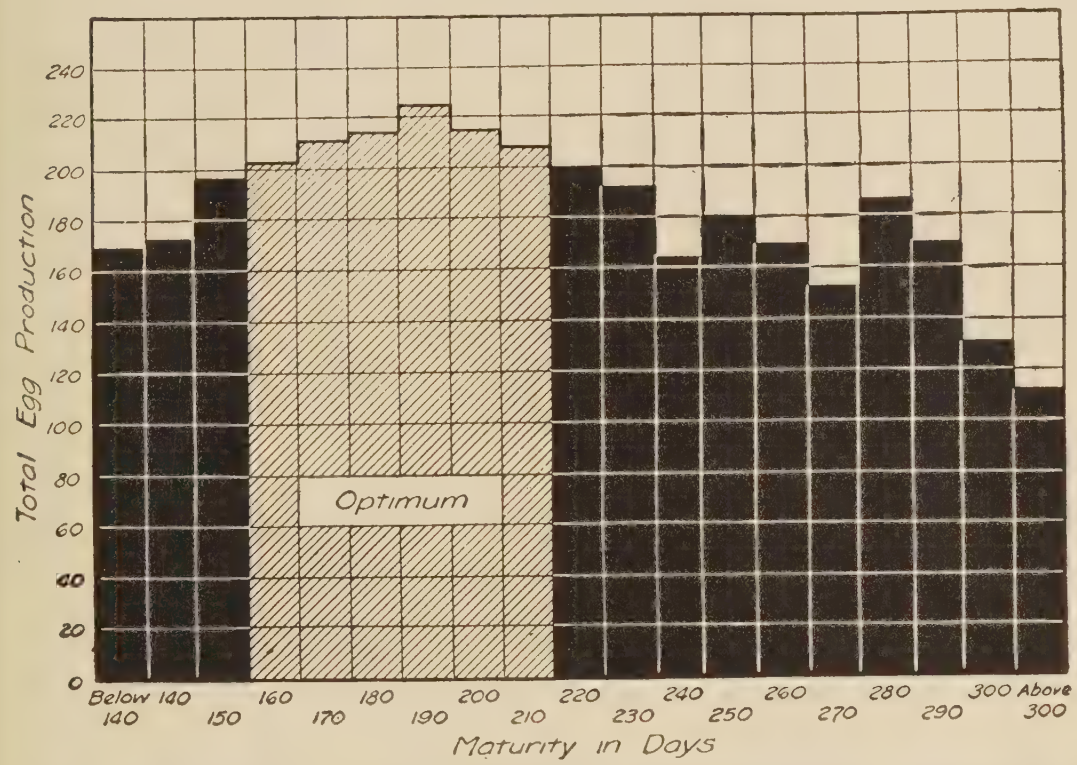

FIG. 51. The highest annual egg production was secured from birds that commenced laying between approximately 160 and 210 days of age in this flock of 684 White Leghorns. (After Knox, 1930*a*.)

Knox (1930*a*) has shown that the best records in egg production for the 684 White Leghorns mentioned previously were made by those birds that commenced laying between 160 and 210 days of age, as shown in Fig. 51.

Marble and Hall (1931) have shown that selection for twenty years in succession of the best layers for breeding purposes in each year's flock of White Leghorns resulted in an increase of 52.24 eggs per bird in the average of the last three years' production over the average of the first three years' production. They concluded that approximately 50 per cent of the increase in egg production was due to earlier sexual maturity, the balance of the increase over the period

of years being due to better management. Petrov (1935), upon an analysis of the Marble and Hall data, concluded that practically all the increase in egg production resulted from improved methods of management and feeding.

The first-year egg-production records of a group of 915 Rhode Island Reds were analyzed by the author from the standpoint of the relationship between age at which laying commenced and annual production, age at which laying commenced being classified on the basis of 10-day intervals, beginning with the period of 150 to 159 days and ending with the period of 230 to 239 days. Thus the table includes only the classes having 20 or more birds in each class according to age at commencement of laying, the total number of birds represented being 915.

TABLE 40. FIRST-YEAR EGG PRODUCTION IN RELATION TO AGE IN DAYS THAT LAYING COMMENCED, IN 915 RHODE ISLAND REDS.

Number of Birds	Mean Age in Days Laying Commenced	Mean Egg Production per Bird
34	155	204
71	164	210
94	175	207
148	185	203
201	194	188
140	204	196
119	214	191
71	224	178
37	234	179

The data in Table 40 indicate that there was relatively little difference in egg production among birds that commenced laying between 150 and 189 days and that their production was only slightly greater than that of the birds that commenced laying between 190 and 219 days.

The importance of early sexual maturity in relation to first-year egg production is clearly indicated in the data by Graham (1932), given in Table 41.

The data in Table 41 show that the best egg-production records were obtained from the birds that commenced laying at approximately 200 days of age. The data also show, however, that the earlier in life that laying commenced, the lower was the first-year mean egg weight

TABLE 41. THE EARLIER IN LIFE THAT LAYING COMMENCED, OR THE SMALLER THE BIRD, THE LESS THE MEAN ANNUAL EGG WEIGHT BUT THE GREATER THE MEAN ANNUAL PRODUCTION IN RHODE ISLAND REDS

(Graham, 1932)

Number of Birds	Mean Age in Days Laying Commenced	Annual Mean Egg Weight in Grams	Body Weight in Pounds	Mean Egg Production per Bird
27	190	52.3	4.50–4.99	227
55	187	53.4	5.00–5.49	214
39	215	55.4	5.50–5.99	204
27	243	57.2	6.00–6.49	169
10	280	58.2	6.50–6.99	133
5	298	58.8	7.00–7.49	121

and the smaller was the size of the bird. The significance of these two factors is discussed in the next chapter.

From the information made available in Fig. 51 and in Tables 40 and 41 it is quite apparent that in order to secure maximum egg production age in days that laying commences is of considerable importance. In general, a first-year record of 200 or more eggs should be attained by Leghorns and general-purpose breeds commencing to lay at approximately 180 and 200 days of age, respectively, or less, provided that such birds do not commence laying too early in the year. Lerner and Taylor (1937) found that age at sexual maturity is superior to date at first egg as a measure of sexual maturity.

Excessively early sexual maturity is detrimental because birds so characterized are usually relatively small in size, as shown in Table 41 and as borne out by the observations of Hays (1933), Waters (1934), and others.

Sexual maturity was found by Knox, Jull, and Quinn (1935) to be among the three most important heritable factors determining egg production in a flock of 903 Rhode Island Reds and in a flock of 884 White Leghorns. For the Rhode Island Reds, the partial correlation coefficient between sexual maturity and annual production was -0.479 and for the White Leghorns -0.398. Lerner and Taylor (1937) also found that sexual maturity in two flocks of White Leghorns, one consisting of 67 and the other of 100 birds, was of considerable importance in determining first-year egg production.

The inheritance of sexual maturity has been undertaken by a number of investigators, Hays (1924) observing that this character

is determined by two dominant genes, one autosomal and the other sex-linked. This observation was confirmed by Waters (1934) as far as the sex-linked gene is concerned and by Warren (1934), for both autosomal and sex-linked genes, although the possibility was suggested that several autosomal and several sex-linked genes may be involved.

Godfrey and Jull (1935) found that in White Leghorn and Rhode Island Red stock with which they worked, the mean sexual maturity of the pullets was significantly correlated with the sexual maturity of their dams. It was also found that sires differed among themselves and dams differed among themselves in their ability to transmit early sexual maturity to their daughters and that full-sisters became sexually mature more nearly at the same age than less related pullets. Hays (1936) concluded that the autosomal and sex-linked genes exercise a cumulative effect in determining sexual maturity.

Inheritance of Rate of Laying. The more eggs a bird lays in a given time the better the rate or intensity of production and the greater the net financial returns in production. It has been found that hens that lay a large number of eggs per clutch are usually better annual layers than birds which lay few eggs per clutch.

It has already been shown in Table 36 that the greater the number of eggs per clutch the shorter the time interval between the eggs of the clutch. Hays (1936*a*), in Rhode Island Reds, found that the shortest interval between eggs in a clutch occurred during the month of April, a time of heavy production, and that short time intervals between the eggs of a clutch were characteristic of birds that laid clutches of many eggs. Hays (1936*b*) found that short intervals between eggs within the clutches were associated with long intervals between clutches and that short intervals between clutches were associated with long intervals between eggs within the clutches. Warren (1936) has shown that when the position of an egg within the clutch is such that laying occurs in the afternoon, the ovulation of the succeeding egg is delayed so that its oviposition occurs in the morning and a new clutch is started. Average clutch size to March first has been used by Hays and Sanborn (1927*a*, 1927*b*) as a measure of rate or intensity of egg laying. Later, Hays and Sanborn (1932) concluded that average annual clutch size was a more accurate criterion of rate of laying than average clutch size to March first.

Another measure of rate of laying that has been used by some workers, Jull (1934), Knox, Jull, and Quinn (1935), Godfrey and Jull (1936) among others, is the number of eggs laid from the time that laying commences in the case of each pullet to March first, the pro-

action being expressed as a percentage of the total number of days volved.

The relationship between rate of production so determined and nnual egg production in a flock of 946 Rhode Island Reds is given in able 42. The data are arranged according to the classes of birds aving a range of 5 per cent in rate of production to March first. he first class of 33 birds had a range in rate from 25 to 29 per cent, nd the last class of 29 had a range in rate from 80 to 84 per cent.

TABLE 42. FIRST-YEAR EGG PRODUCTION IN RELATION TO RATE OF PRODUCTION IN RHODE ISLAND REDS

Number of Birds	Mean Rate of Production	Mean Egg Production per Bird
33	27	144
45	32	147
76	37	161
73	42	168
93	47	173
92	52	189
85	57	200
95	62	204
148	67	206
103	72	220
74	77	227
29	81	241

The data in Table 42 show that the higher the rate of production from the date of first egg to March first, the higher the annual egg production. By using the same measure of rate of production, except that all pauses for four or more consecutive days between November first and March first were omitted from the calculations, Hays and Sanborn (1927*a*) obtained a coefficient of correlation of 0.48 ± 0.01 between rate and annual production among 2,528 Rhode Island Reds. Knox (1927) obtained a coefficient of correlation of 0.34 ± 0.08 between the rate of production during the two consecutive months of highest production and annual production among 91 White Plymouth Rocks. Knox, Quinn, and Jull (1935) obtained a partial correlation coefficient between rate of production and annual production of 0.555 and 0.568, respectively, among 903 Rhode Island Reds and 884 White Leghorns.

An analysis of the production records of a highly restricted group of 578 White Leghorns, led Lerner and Taylor (1936) to conclude

that, if rate of laying is controlled by the same genes throughout th year, the logical method of determining rate is to exclude from th calculation all periods of pauses in egg production. In their study o the problem of rate of laying, Lerner and Taylor eliminated al pauses caused by broodiness and all other pauses of seven or mor consecutive birds, and, for purposes of determining the winter rate they subtracted the number of days from November first to the dat of the first egg in the case of birds commencing to lay after Novembe first. This method of determining the winter rate of laying wa employed by Hays and Sanborn (1923).

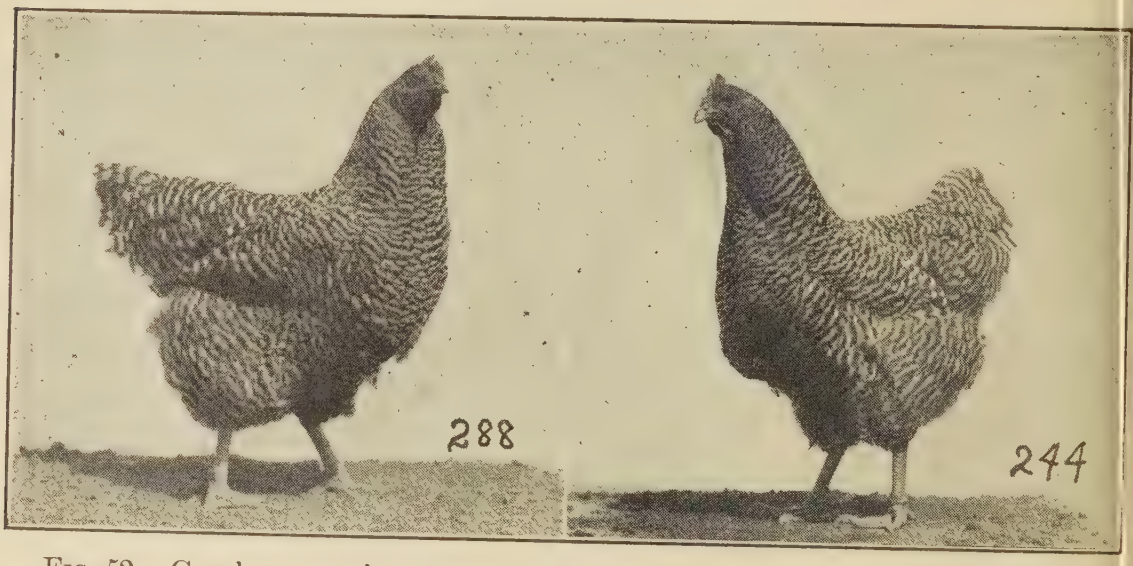

FIG. 52. Good egg production, as indicated by the records of 288 and 244 eggs in Barred Plymouth Rocks or any variety of any breed is largely a matter of good breeding, providing the methods of feeding and management are satisfactory. (Photo by U. S. D. A.)

Lerner and Taylor (1936) suggested the possibility that winter and spring rates of laying may be controlled by the same genes. Lerner and Taylor (1937) concluded that the winter or spring rate of laying served as a more accurate criterion of annual egg production than summer and fall rates of laying.

The problem of most logically determining the rate of laying or the rate of egg production is probably largely a matter of judgment. The mean size of clutch for the year is certainly a measure of the rate of laying, particularly when pauses on account of broodiness or for other causes are eliminated from the calculation. The percentage of eggs produced during relatively short periods, pauses from all causes being eliminated, also represents rate laying for those particular periods. On the other hand, the percentage of eggs produced during a given period, including broody and other pause days, represents rate of production for that period. All measures of determining rate

ve their arbitrary features, but, for all practical purposes, they are ually serviceable in demonstrating the fact that laying birds differ nong themselves in rate of laying and in rate of production and that proper selection and breeding methods rate can be increased.

For instance, Hays and Sanborn (1927) have shown that rate of ying in terms of winter clutch size is inherited, and Godfrey and Jull 936) have shown that rate of production from the date of the first g to March first is inherited. It was found that full-sisters laid at ore nearly the same rate than half-sisters and that half-sisters laid more nearly the same rate than unrelated birds. There may be ecific genes that determine the rate of laying at different periods ring the first year and there is in all probability a large number of nes that determine the rate of production from the date of the first g to the date of the last egg of the first-year production.

Inheritance of Broodiness. In Leghorn, Ancona, and a few her breeds, broodiness is relatively rare. On the other hand, in lymouth Rock, Rhode Island Red, New Hampshire, and many other reeds, the degree of broodiness in a flock may vary from a few birds oing broody once to many birds each going broody several times. roodiness is of economic importance because it is usually accompanied y cessation of egg production.

That the amount of broodiness in a flock can be reduced materially y the adoption of proper selection and breeding methods has been hown by Hays (1939) with a flock of Rhode Island Reds under prac- ically the same system of breeding from 1916 to 1937. In 1916, more han 86 per cent of the females were broody during the first-laying ear, whereas in 1937 only slightly over two per cent of the females ere broody. Throughout the entire period, however, the average umber of days on nonproduction associated with broodiness remained airly constant at approximately fifteen days.

Knox, Jull, and Quinn (1935) found that in a flock of Rhode Island Reds, broody birds started to lay later in life, laid at a relatively lower rate, and were less persistent in production than nonbroody birds.

The heritable nature of broodiness was apparently first demon- strated by Goodale, Sanborn, and White (1920) in a flock of Rhode Island Reds. Based on their results, they concluded that broodiness depends upon two complimentary genes dominant to nonbroodiness. Neither gene by itself produces broodiness. It was found that, when some males were mated to nonbroody females, certain of the nonbroody females produced daughters that exhibited broodiness, whereas certain other nonbroody females produced daughters none of which exhibited

broodiness. These results suggest the complementary nature of the genes for broodiness, one of the genes being introduced by the sire and the other by the nonbroody dams that produced broody daughters. Other matings consisting of broody females and any kind of males always produced some broody daughters, showing that broodiness is dominant to nonbroodiness.

Punnett and Bailey (1920) concluded that broodiness is apparently due to more than one independent autosomal gene. Warren (1930) made reciprocal matings between White Leghorns and Rhode Island Reds and observed considerable difference in the amount of broodiness between the daughters of the two matings. The difference was felt to be due to variation in the degree of broodiness in the parental stocks. Roberts and Card (1933) made reciprocal matings between White Leghorns and Dark Cornish and observed that the two matings produced quite different results with respect to the amount of broodiness exhibited by the daughters. The mating of White Leghorn sire × Dark Cornish dams produced daughters 37 per cent of which were broody an average of 2.1 times. The mating of Dark Cornish sire × White Leghorn dams produced daughters 88 per cent of which were broody an average of 3.7 times. The results secured from these matings between a relatively nonbroody and a broody breed, demonstrate that at least one sex-linked gene is involved in the inheritance of broodiness.

Inheritance of Winter Pause. Sometimes pullets, especially early hatched and precocious ones, will lay for a certain time during the late summer and early fall and then will stop laying for a period, the length of which may vary considerably. This pause in production Hays (1925) has referred to as the "winter pause." Other pauses sometimes occur, both in spring and summer. These pauses in production are not to be confused with intervals between clutches although it is often difficult to determine what constitutes a legitimate pause as compared with a normal clutch interval. By some investigators, a period of seven consecutive days has been arbitrarily designated as a "pause."

Whether or not such pause periods may be regarded as biological entities that are inherited as such is perhaps a debatable question. Certain it is that many pauses in production are due entirely to physical condition and environmental circumstance. Some hens stop laying temporarily because of a slight infection of coryza or "cold," or because of indigestion, or because of an abrupt change in temperature, or because of a frosted comb, or because of one or more other things that may *happen* to several members of the flock. Still other complications

e involved in determining the probable causes of all pauses inasmuch some short pauses are associated with an unobserved slight degree molting or with a mild form of broodiness, two complex physio-gical processes the occurrence of each of which is conditioned by rmones and genes. Other pauses which occur, however, may not be fluenced by specific hormones or genes. It is felt, therefore, that uch more work is necessary before any definite period of time can established as a biological entity or as a measure of heritable fferences in resistance or susceptibility to changes in environmental nditions.

Hays (1924), working with Rhode Island Reds, suggested that a riod of seven or more consecutive days of nonproduction should be garded as a winter pause. Hays (1936), however, used four or ore consecutive days of nonproduction as a winter pause, and among her observations, concluded that pauses of less than seven days are obably due to different causes than are longer pauses. It was also inted out that short intervals between eggs within a clutch and a gh rate of laying before pause occurred had a tendency to shorten e pause and that a relatively high rate of laying was more likely follow a short pause than a long one.

Using seven days as a measure of pause, Lerner and Taylor (1936) udied the relationship between pauses and rate of laying in a highly lected flock of White Leghorns. It was found that the occurrence winter pause did not affect winter rate of laying and that, with a w exceptions, the rate of laying both before and after a pause emed to be somewhat depressed. Lerner and Taylor (1939) found at in two groups of White Leghorns, the degree of pausing was fluenced by the genetic constitution of the birds, the date of hatch, nd the season.

Until more is known concerning the cause of pauses, especially hort ones, other than those associated with broodiness and molting, ractically nothing can be said regarding their inheritance.

Inheritance of Persistence. The longer that egg production is ontinued prior to the first annual adult molt, the greater the total f the first-year egg production. Persistency of production simply mplies that a bird continues to lay well toward the close of her first-aying year, cessation of production usually being followed by a omplete molt.

It is obvious, of course, that the earlier that molting takes place, he shorter the period of first-year production. Hendricks (1933) has hown that among White Leghorns which commenced their first-year

annual molt relatively early the duration of the molt was longer tha among late molters.

It has been definitely established that the termination of the firs year of laying is intimately associated with the onset of the firs annual molt, except that a few birds have been known to contin laying throughout the entire period of molting. The process of moltin includes the dropping and renewal of the plumage. In persisten producers, molting takes place much later than in nonpersistent pro ducers, presumably because the activity of the sex glands tends t inhibit the onset of the molting process.

A suitable criterion of persistency for the purpose of determinin the mode of its inheritance has been difficult to decide upon by th various workers interested. Goodale (1918) suggested age at last eg or date at last egg. Hays and Sanborn (1926) classified Rhode Island Reds as persistent producers if they laid for 315 days or more fro the date of the first egg. Hays (1927) obtained a high positive correla tion between total first-year production and persistency, indicatin that the best producers are usually late molters, an observation con firmed by Hays and Sanborn (1933). Hays and Sanborn (1930) studied the relationship between the duration of the molt and per sistency and found that the nonpersistent group of birds had an aver age molting period of 93.5 days, whereas the persistent group had a average molting period of 72.94 days. Hays (1936*b*) crossed tw lines of Rhode Island Reds differing by approximately 90 days wit respect to the length of period of laying before molting occurred an found that the dividing point between high and low persistency phenotypes lies close to 270 days. It was suggested that high per sistency depends upon a single dominant autosomal gene. Hays an Sanborn (1939) recommend that no females should be used as breeder unless they have laid for at least a 300-day period.

A method of measuring persistency that has sometimes been employed is by the number of eggs laid during the last 50 days of th first-laying year. The data in Table 43 show that those birds which laid best during the last 50 days of the first-laying year were also th best annual layers.

Since the matter of determining the number of eggs laid per bird during the last 50 days of the first year of laying in a large flock involves much time and labor in examining the records, it was decided to establish a more practical basis for selecting the birds of a flock on the basis of persistency of production. Accordingly, 906 Rhode Island Reds were classified into groups on the basis of the average number of eggs laid during August and September, the birds being

ɔuped on the basis of five-egg intervals. Some of the early-maturing rds may have finished their first-year production prior to August, t despite this possibility the data given in Table 43 show that those rds which laid best during August and September were also the

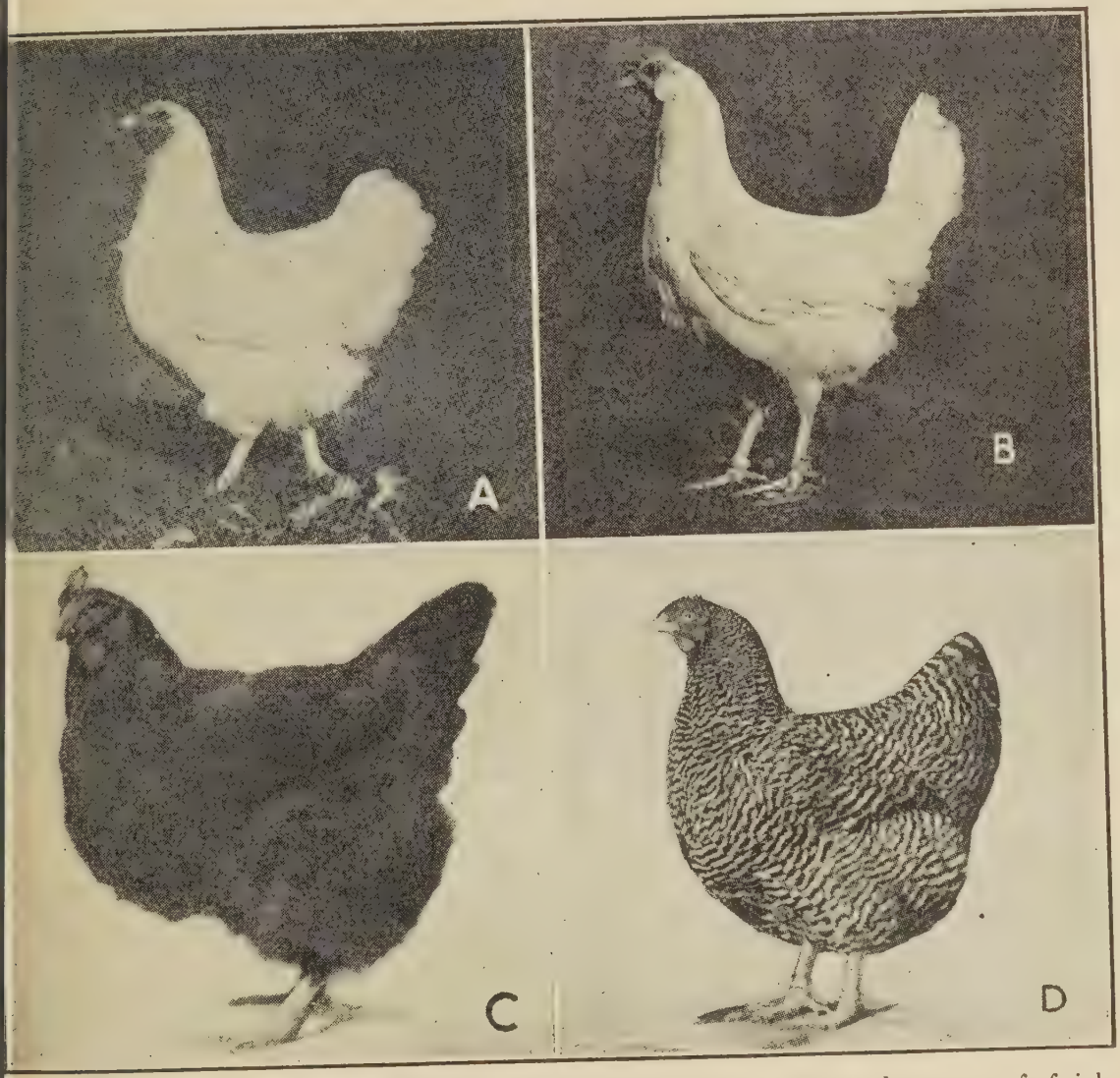

FIG. 53. Records of 300 eggs or more in one year have become of fairly common occurrence during recent years. A, White Wyandotte that laid 305 eggs in a Storrs international egg-laying contest. (Photo by Storrs Agr. College.) B, White Leghorn that laid 351 eggs, 223 of them consecutively, in a Canadian egg-laying contest. (Photo by Univ. of British Columbia.) C, Black Orpington that laid 354 eggs in an Australian egg-laying contest. (Photo by P. Rumball.) D, Barred Plymouth Rock that laid 358 eggs at the University of Saskatchewan, Canada. (Photo by Univ. of Sask.)

birds that laid best during their first year of laying, regardless of when first-year production ceased in the case of each bird. It is apparent, therefore, that egg production during August and September serves as a practical method of determining the most persistent producers.

Knox, Jull, and Quinn (1935) found that in the case of a flock of White Leghorns and a flock of Rhode Island Reds with which they

TABLE 43. MEAN FIRST-YEAR EGG PRODUCTION IN RELATION TO THE MEA PRODUCTION PER GROUP DURING THE LAST 50 DAYS OF THE FIRST-YEAR PRO DUCTION AND DURING AUGUST AND SEPTEMBER IN RHODE ISLAND REDS

Number of Birds	Mean Egg Production Last 50 Days	Mean First-Year Egg Production	Number of Birds	Mean Egg Production August-September	Mean First-Year Egg Production
139.....	0	149.95	47	0	139.02
108.....	2.25	163.36	61	2.51	153.48
76.....	8.07	178.97	56	8.16	166.43
96.....	13.36	179.89	104	13.15	169.17
112.....	17.80	191.95	115	18.20	173.59
105.....	22.98	203.04	114	23.11	187.56
113.....	27.92	220.70	103	28.05	198.93
103.....	32.91	234.26	103	33.05	215.55
42.....	37.57	236.64	109	37.85	221.36
———	———	———	64	42.52	236.66
———	———	———	30	47.53	247.33

worked the number of eggs laid during the last 50 days of the first-laying year and the number of eggs laid during August and September of the year following date of hatch were similar measures of persistence of production. The number of eggs laid during August and September was somewhat the better measure of persistency and is, of course, a much simpler measure to apply. The partial correlation coefficient between this measure of persistency and annual egg production was + 0.733 for White Leghorns and + 0.722 for Rhode Island Reds, giving persistency more significance than other characters.

Lerner and Taylor (1937) used age at last egg and date of last egg as measures of persistency among the members of a White Leghorn flock. Date at last egg proved to be a better measure of persistency than age at last egg, and Lerner and Taylor (1938) observed that age at last egg is the most important single character among those that determine the number of eggs laid during the first laying year.

The Genetics of Egg Production. It has already been shown that a study of the inheritance of egg production is an extremely complicated problem, since the formation and elaboration of eggs involves several complicated physiological processes, the number of eggs laid being conditioned by other physiological processes, including broodiness and molting, and since environment exercises a pronounced influence. No wonder that comparatively little is known concerning

the genetics of egg production. Hays (1924, 1927) and Hays and Sanborn (1939) have suggested that a total of eight pairs of genes are primarily responsible for the manifestation of five characters, which, in their opinion, are primarily responsible for determining egg production, whereas Munro (1936) has suggested that probably several hundred pairs of genes determine the number of eggs laid by a bird.

The three characters that have been found to be of greatest significance in influencing egg production are sexual maturity, rate of laying, and persistency of production. Hays (1927) concluded that linkage existed between the gene for persistency and the autosomal gene for sexual maturity, but Knox, Jull, and Quinn (1935) and Lerner and Taylor (1937*b*) questioned the existence of such linkage, and Hays (1939) finally concluded that the genes for sexual maturity and for persistency are inherited independently. Knox, Jull, and Quinn (1935) supplied evidence which suggests that approximately 70 per cent of the variation in the individual first-year records of a flock of White Leghorns and Rhode Island Reds was due to these three characters and that some of the variation common to each character was genetic in nature. Lerner and Taylor (1937*a*) came to the conclusion that from 55.3 to 91.4 per cent of the variation in egg production records of their White Leghorn flock was accounted for by the three same characters and that the variation of these characters was genetic in nature to a considerable degree.

At the same time, Munro (1936) concluded that the mechanism of egg production is so complex and involved that a specific analysis of the mode of inheritance either of yearly egg production or of its component parts is practically impossible in the present state of knowledge. Evidence was presented indicating a gene-gene as well as a gene-environment interaction in affecting egg production, and it was finally concluded that only from 20 to 25 per cent of the observed variance among populations is due to gene segregation and recombination, environmental influences causing a relatively greater proportion of variation in egg production between individuals and among families than does inheritance.

Effects of Inbreeding on Egg Production. The effects of inbreeding on egg production are of particular importance to poultry breeders because they wish to know whether or not the mating together of closely related males and females from their best layers will tend to produce uniformly high egg producers. The question in the mind of the average poultry breeder is whether or not inbreeding will tend to develop heavy laying as a fixed character in his strain.

The results secured by Dunn (1923), Hays (1924, 1929), and

Dunkerly (1930) show that close inbreeding effects a decrease in egg production. Similar results were also secured by Jull (1932), who observed that close inbreeding tends to increase the age in days at which laying commences.

TABLE 44. FIRST-YEAR EGG PRODUCTION AS AFFECTED BY THREE YEARS OF BROTHER × SISTER MATINGS IN WHITE LEGHORNS

(Jull, 1932)

Mating	Pen 1	Pen 2	Pen 3	Pen 4
Outbred ancestors, 1926.....	168	219	220	213
First-year inbred birds, 1927...	143	159	197	152
Second-year inbred birds, 1928.	129	119	173	161
Third-year inbred birds, 1929...	76	80	139	173

The significant fact brought out in Table 44 is that the first year of brother × sister mating resulted in a marked decrease in egg production and that the second and third years of brother × sister matings resulted in a still further decline in egg production except in the case of Pen 4, which was perhaps due to chance. The data show that families of birds react differently under similar methods of inbreeding.

Four years of inbreeding Rhode Island Reds led Hays (1934) to conclude that inbreeding retarded sexual maturity, increased the percentage of birds with winter pause, reduced rate of laying, and decreased persistency but had no effect on broodiness. The progeny of different inbred males differed considerably, according to Hays (1935). The daughters of noninbred males laid an average of 226 eggs, whereas the daughters of inbred males laid an average of 209 eggs.

The effects of two different forms of inbreeding on egg production were reported by the British Ministry of Agriculture and Fisheries (1934) for White Wyandottes, Rhode Island Reds, and White Leghorns. In Table 45 are given the average first-year annual records of egg production among the progeny secured from father-daughter outbred, father-daughter-inbred, and control matings. The first two matings are forms of inbreeding. The father-daughter outbred mating consisted of mating a cockerel to unrelated pullets, then mating the same male the next year to the female progeny secured from the first mating. The father-daughter inbred mating consisted of selecting a cockerel from a family produced by the original mating and mating him with his sisters and the next year he was mated to his female progeny.

TABLE 45. AVERAGE EGG PRODUCTION OF DAUGHTERS OF FATHER-DAUGHTER OUTBRED, FATHER-DAUGHTER INBRED, AND CONTROL MATINGS

(British Ministry of Agriculture, 1934)

Breed	Father-Daughter Outbred and Control Matings		Father-Daughter Inbred and Control Matings	
	F. D. O.	Control	F. D. I.	Control
White Wyandottes	161	199	155	191
Rhode Island Reds	135	160	142	160
White Leghorns	131	135	127	150

It is to be observed from the data in Table 45 that the average egg production of the progeny of both forms of inbred matings was lower than that of the progeny of the control matings.

The results of inbreeding six families of White Leghorns over a period of ten years by Waters and Lambert (1938) showed that as the coefficient of inbreeding increased, the average annual egg production tended to decrease slightly. All birds in the last year of the experiment were descended from four males and seven females, and coefficients of inbreeding ranged from 41 to 82 per cent.

The results secured from the various lines of inbreeding experiments mentioned previously show that in all cases egg production was affected adversely. It should be pointed out, however, that in none of the experiments was there a conscious attempt to select the breeding stock used each year with the specific objective of improving egg-laying ability. Had the selection of breeding stock been practiced on this basis, the results secured might have been quite different.

Effects of Crossbreeding on Egg Production. Relatively few experiments have been conducted with a view of determining the effects of crossbreeding on egg production. Warren (1927) crossed White Leghorns and Jersey Black Giants and observed that the crossbred progeny laid somewhat better than the purebred progeny. Warren (1930) crossed White Leghorns and Rhode Island Reds and observed that the average egg production of the progeny of each of the different matings was as follows: White Leghorn male × White Leghorn females, 212; Rhode Island Red male × Rhode Island Red females, 169; White Leghorn male × Rhode Island Red females, 215; and Rhode Island Red male × White Leghorn females, 199.

Knox and Olsen (1938) crossed White Leghorn males with Rhode Island Red females and observed that the crossbred progeny laid an average of 145 eggs compared with an average of 201 and 203 eggs, respectively, for the purebred White Leghorn and Rhode Island Red progeny. When several other crosses involving Barred Plymouth Rocks, Rhode Island Reds, and White Wyandottes were made, the results secured indicated that they are influenced to a considerable extent by the quality of the parental stocks used and that crossbreeding increases broodiness in the crossbred progeny. The average egg production of the progeny of all the crosses involving general-purpose breeds was 166, compared with 139 as the average egg production of the progeny between White Leghorns and the general-purpose breeds.

Knox (1939) secured the results given in Table 46 from the progeny of crosses between Rhode Island Red males and Light Sussex and White Wyandotte females, respectively.

Table 46. Average Egg Production of the Progeny of Purebred and Crossbred Matings

(Knox, 1939)

Mating	Number of Progeny	Average Egg Production
Rhode Island Red ♂ × Rhode Island Red ♀	234	202
Light Sussex ♂ × Light Sussex ♀	335	134
White Wyandotte ♂ × White Wyandotte ♀	80	142
Rhode Island Red ♂ × Light Sussex ♀	366	168
Rhode Island Red ♂ × White Wyandotte ♀	217	161

The data given in Table 46 show that the egg production of the crossbred progeny was approximately midway between the egg production of the Rhode Island Red progeny on the one hand and the Light Sussex and White Wyandotte progeny on the other hand.

The effects of crossing of highly inbred lines of the same breed were observed by Jull (1932). Four inbred lines of White Leghorns that had been brother × sister mated for three years were crossed and in every case except one, the crossed inbred pens laid better than the third-year inbred pens. It should be noted, however, that the average annual egg production of the third-year inbred pens was relatively low. Crossbreeding brought together desirable genes isolated by inbreeding.

THE POSSIBILITIES OF INCREASING EGG PRODUCTION BY BREEDING

In spite of the possibilities of improving egg production through the intelligent selection and mating of breeding stock, the fact remains that the average egg production per bird of the laying stocks of all countries is very low. In every country too many poor producers are reared each year, and too many of these poor producers are used as breeders. Many poultrymen fail to realize that mediocrity tends to reproduce itself.

Although egg production is inherited, progress in developing a "bred-to-lay" flock may be relatively slow because of the number of factors involved. In the first place, the inheritance of egg production has been shown to be a complex problem, involving such factors as sexual maturity, rate of laying, freedom from broodiness, and persistence of production. There is also to be considered the influence on egg production of various hormones secreted by the endocrine glands. In addition, the influence of environmental factors, including the kind of diet fed the laying stock, are frequently quite pronounced with respect to their effects on egg production. Munro (1937) has expressed the viewpoint that most of the increase in egg production that has taken place in the flocks of a country during recent years has been due to nongenetic causes.

The results secured in egg-laying contests held in various parts of the world demonstrate the possibilities of increasing egg production, whether by an improvement in environmental conditions or by the adoption of improved breeding practices, or both. Apparently the first organized laying contests were held in England, for Brown (1930–1931) has stated that the first "laying trials" were held in that country in 1897. These trials were for short periods only, but they were followed by trials of about a year's duration, the first of which began in 1912. From that time on, an officially conducted laying contest has been held every year at the Harper Adams Agricultural College. The first twelve-month laying contest was inaugurated, however, in 1902 in New South Wales, Australia, and was held at the Hawkesbury Agricultural College. The first officially conducted egg-laying contest in North America was inaugurated in British Columbia, Canada, in October, 1911, and the second one was inaugurated in the United States at the Storrs Agricultural College in November, 1911. During the past decade egg-laying contests have been held in several countries.

Four things in particular have been brought forcibly to the attention of poultrymen through the results secured at the laying contests:

1. A pen of ten birds in a contest frequently averages over 250 eggs per bird in a year.

2. It has been shown that among 100 pens in any one contest there is usually great variation in laying ability, some pens averaging as many as 100 eggs per bird more than others.

3. Improved methods of feeding and management, including the use of artificial lights, during recent years have resulted in securing higher average egg-production records quite independent of any improvement in breeding quality that may have taken place.

4. The most progress in breeding for increased egg production has been made with varieties such as White Leghorns, Black Langshans, Australorps, White Wyandottes, and Rhode Island Reds. In other words, in parti-colored varieties, where the poultry breeder has to select his breeding stock on the basis of perfection in color pattern in addition to egg-laying ability, an additional burden is added to the breeding program that may do much to prevent progress in dealing with characteristics of economic value.

Since three of these egg-laying contests have been running for a considerable number of years, it is interesting to compare the results at intervals. The data are given in Table 47. The records of the leading varieties only were selected. The average annual egg production per bird for a period of three consecutive contest years was determined; then, following an interval of several years, another average was determined for another three consecutive contest years. In the case of the Australian contest conducted at Hawkesbury Agricultural College, there is an interval of approximately 25 years between the two averages determined; in the case of the United States contest conducted at Storrs Agricultural College, the interval between the two averages is approximately 15 years; in the case of the English contest conducted at Harper Adams Agricultural College, the interval between the two averages is approximately 10 years.

The data given in Table 47 show that in each of the three varieties of Australian birds, there was an increase in the second 3-year average over the first 3-year average as follows: White Leghorns, 2 eggs; Black Langshan, 28 eggs; Black Orpingtons, 27 eggs. It is to be noted that the White Leghorn level of production during the first 3-year period was comparatively high—so high that after approximately 25 years the level was raised but 2 eggs per bird. Because the Black Langshan and Black Orpington level of production during the first 3-year period was lower than the White Leghorn level, greater progress was possible; during the 25-year interval the black varieties caught up to the White Leghorns.

During the first 3-year period the level of egg production of the three American varieties was comparatively low, so that in an interval of 15 years a considerable increase could be achieved in each of the three varieties. As a matter of fact, starting on a lower level than the birds in other contests, the Storrs averages for each of the three varieties exceed by a considerable margin the averages obtained at the other two contests during the last 3-year period.

TABLE 47. THE AVERAGE ANNUAL EGG PRODUCTION PER BIRD FOR EACH OF TWO 3-YEAR PERIODS FOR THE LEADING VARIETIES IN AUSTRALIAN, UNITED STATES, AND ENGLISH EGG-LAYING CONTESTS

Item	White Leghorns	Black Langshans	Black Orpingtons
Australia (Hawkesbury Agricultural College):			
3 years, 1908–11	192	171	173
3 years, 1932–35	194	199	200
	White Leghorns	Barred Plymouth Rocks	Rhode Island Reds
United States (Storrs Agricultural College):			
3 years, 1915–18	159	169	157
3 years, 1930–33	235	217	220
	White Leghorns	White Wyandottes	Light Sussex
England (Harper Adams Agricultural College):			
3 years, 1922–25	186	186	169
3 years, 1931–34	187	192	166

William F. Kirkpatrick, in charge of the Storrs contest, has stated that during the last three years recorded in Table 47 the average egg production of each pen of 13 birds was determined on the records of the 10 highest ones. Since 1922 artificial lights have been used in the laying pens from 9 to 10 P.M. daily, and during the past seven or eight years the New England conference rations have been used, subject to slight changes from time to time. The extent to which these modifications in computation and management account for the increase in the level of egg production cannot be determined, but it may be safely assumed that during the last fifteen years there has been a substantial increase in the laying ability of the birds entered in the contests.

During an interval of ten years in the English contest, there was little change in the level of egg production of the three varieties.

It should be pointed out in connection with the results secured at egg-laying contests conducted over a period of years, that not all of the increase in egg production achieved is due to the breeding methods followed by the breeders who enter birds in the contests. Indeed, in many contests a great deal of the increase in levels of egg production has been due to improved methods of selecting the entrants and feeding and management at the contests.

It is impossible to decide whether the environmental or nongenetic factors have exercised the major influence in the increased level of egg production that has occurred in the laying contests over a period of years.

It is known, however, that in the American contests, at least, during the latter years of the egg-laying contests there was an increased proportion of birds entered by the leading breeders of the country, the birds entered representing a highly selected population of specially selected birds developed by progressive breeding methods.

Many genes are involved in the inheritance of egg production, including a sex-linked gene for earliness of sexual maturity and a sex-linked gene for broodiness. In spite of the fact that the mode of inheritance of egg production has not been determined, it is obvious that it is possible to increase laying ability by the adoption of a sound selection and breeding program. The most intelligent procedure to be followed in the adoption of such a program is outlined in Chapter IX. It should be pointed out at this time, however, that the number of eggs produced is not the only criterion of a wellbred flock, for egg weight and quality should also be taken into consideration, as outlined in the next chapter.

In spite of the fact that egg-laying contests were apparently started for the purpose of encouraging the adoption of sound breeding programs by poultry breeders, the contests have several shortcomings. There is no denying the fact that the results of the contests have frequently been used primarily for propaganda purposes. In many cases the record of production of a pen of birds entered by a poultry breeder was not at all representative of the breeding worth of even a portion of his home flock. Entirely too much publicity has been given to high individual records of production. Although egg production and egg weight are taken into consideration, practically none of the contests has considered such important characteristics as shell color in White Leghorns, shell texture, interior egg quality, and the viability of the stock.

PROBLEMS

1. What are some of the more important physiological aspects of egg production?

2. In conducting breeding work for the purpose of determining the nature of the inheritance of egg production, what are the more important external factors affecting egg production that should be kept as uniform as possible from year to year?

3. Discuss the significance of available evidence concerning whether or not egg-laying ability in the domestic fowl has been increased during the past twenty years.

4. Discuss the more important factors that should be kept in mind in determining the proportion of pullets that should comprise the laying flock; discuss the decline in egg production that would probably occur in a given flock of pullets.

5. Discuss the relative merits of three theories of the Mendelian inheritance of egg production that have been proposed.

6. From the standpoint of securing maximum egg production, what is approximately the best time to hatch pullets in different parts of the northern and southern hemispheres?

7. In relation to total first-year egg production, of what significance is age in days that laying commences, and at approximately what age should pullets of the various breeds commence laying?

8. Of what relative importance is rate of egg production, and what are some of the most practical ways of determining rate?

9. What is the relationship between age in days that laying commences and persistency of production, and what is one of the most practical ways of selecting layers on the basis of persistency of production?

10. Outline a breeding program that should enable the poultry breeder to improve egg production from year to year.

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CHAPTER VIII

THE INHERITANCE OF EGG CHARACTERISTICS

The inheritance of egg-laying ability has been discussed in Chapter VII, but there are other things besides the number of eggs produced that every poultryman should take into consideration. The eggs laid should be of good marketable size, of good shape for packing in cartons and cases, uniform in color, of good shell texture to withstand breakage under ordinary methods of marketing, and of good quality of yolk and albumen.

These various egg characteristics are all of considerable economic importance. For instance, a hen may lay a large number of eggs, but most of them may be small, thus commanding a lower price than fewer eggs most of which are of good size. Then again, a hen may lay eggs of good size and shape, but they may have poor shell texture so that many of them break when shipped to market. The quality of the yolk and albumen is important, especially from the standpoint of the keeping quality under normal conditions of storage. To whatever extent these various egg characteristics are inherited, it becomes important for the poultry breeders to give them due consideration in the selection of breeding stock from year to year.

THE INHERITANCE OF EGG WEIGHT

Egg size and egg weight are synonymous terms so far as new-laid eggs are concerned. The larger the size, the heavier the egg. On the other hand, among stale eggs a large egg may be much lighter in weight than a smaller one because of the loss through the porous shell of much of the water from the albumen and yolk. Various investigators, however, have used the terms "size" and "weight" interchangeably in discussing the inheritance of egg size. In a large measure such practice is justified in view of the fact that inheritance studies always involve new-laid eggs, which lose very little water from the time they are laid to the time they are weighed. Moreover, Pearl and Surface (1914) have shown that either weight or bulk may be used as a measure of size. The weight of an egg is the most easily obtained criterion of size so that inheritance studies usually deal in terms of egg weight.

The standard weight of an egg is 2 ounces, and, from the standpoint

of meeting market requirements, it is obvious that poultrymen should endeavor to maintain flocks whose individual members lay eggs of approximately standard weight. In practically all studies on the inheritance of egg weight, the weights are given in grams, a 2-ounce egg weighing 56.7 grams.

Some interesting records have been reported by Kohmura (1931) for a number of fowls in Manchuria that are noted for the very large eggs they lay. Among 25 birds secured by the Manchurian Agricultural Experiment Station, 12 laid eggs averaging 63.5 to 69.0 grams each, 10 laid eggs averaging 70.0 to 79.0 grams each, and 3 laid eggs averaging 80.0 to 86.0 grams each. The next year a pullet laid eggs up to 113.0 grams (practically 4 ounces) in weight and two years later 4 pullets laid eggs averaging over 85.0 grams each for the yearly production of each bird.

Before the results of studies on the inheritance of egg weight are discussed it is advisable to discuss the various factors that may affect egg weight.

Egg Weight in Relation to the Weight of the Different Parts of the Egg. Obviously, the total weight of an egg is determined by the collective weights of its component parts. The contribution that each major part of the egg makes toward the weight of the whole egg is shown in Table 48, according to the observations of different investigations.

TABLE 48. PERCENTAGE OF MAJOR PARTS OF EGG IN RELATION TO THE WHOLE EGG

Investigator	Albumen	Yolk	Shell
Curtis (1911)	59.26	29.14	11.18
Jull (1924*a*)	58.43	30.99	10.58
Asmundson (1931*a*)	58.76	30.01	10.50
Bennion and Warren (1934)	58.57	31.50	9.91

It has been determined, however, that the percentage weights of the different parts of the egg and the weight of the egg itself vary during the first-year production of any individual bird. It might also be pointed out that the percentages of the parts of the egg may apparently be influenced by the relative size of the egg. Asmundson (1933) found, for instance, that among eggs averaging 46.14 grams per egg the percentage of each of the parts was: albumen, 61.62; yolk, 27.42; shell, 9.90.

From studies on the relationship between egg weight and egg shape by Pearl (1909), Curtis (1914*b*), Pearl and Curtis (1914), and more particularly Pearl and Surface (1914), it has been shown that egg weight is more highly correlated with egg breadth than with egg length. This observation has been confirmed by Asmundson (1931*a*), who also found that albumen weight and shell weight are each more highly correlated with egg breadth than with egg length. Asmundson found that, although yolk is somewhat more highly correlated with egg breadth than with egg length, the difference was not significant.

Breed and Egg Weight. Since the standard weight of pullets of two breeds sometimes differs markedly, 4 pounds for White Leghorns and 6 pounds for Plymouth Rocks, and since egg weight is, in general, correlated with body weight, as shown in subsequent discussion, it might be assumed that birds belonging to two different breeds would lay eggs differing significantly in weight. That such is not the case, however, is shown by the observations of Funk and Kempster (1934) and Hall (1939).

Funk and Kempster (1934) pointed out that within any given breed there is wide variation in the weight of eggs produced; they also showed that among the breeds from which they made egg-weight observations, the relative order of those laying the heaviest eggs to those laying the lightest eggs was as follows: Rhode Island Reds, Plymouth Rocks, Anconas, Wyandottes, and White Leghorns. Among representatives of four different breeds, Hall (1939) found that the relative order was as follows: Plymouth Rocks, Wyandottes, Leghorns, and Rhode Island Reds. It is clearly apparent from this as well as from the observations of practical poultrymen, that it is not so much the question of breed in relation to egg weight as the breeding of the birds within a breed.

Egg Weight in Relation to Body Weight. That a relationship exists between body weight and egg weight has been demonstrated by a number of workers. In a flock of White Plymouth Rocks, Hadley and Caldwell (1920) observed that the larger birds tended to lay the heavier eggs, although in another flock there seemed to be no such relationship. Asmundson (1921) found the weight of the egg to be positively correlated with the body weight in White Leghorns. Atwood (1923), also with White Leghorns, observed that there was a significant correlation between the monthly mean body weight and the monthly mean egg weight.

Jull (1924*b*) reported a coefficient of correlation of $+0.34 \pm 0.09$ between maximum body weight and mean egg weight in a group of 40 Barred Plymouth Rock pullets. Atwood (1925) observed that

among his White Leghorns the heavier birds laid the larger eggs. Parkhurst (1926), using White Leghorns, corroborated Jull's findings

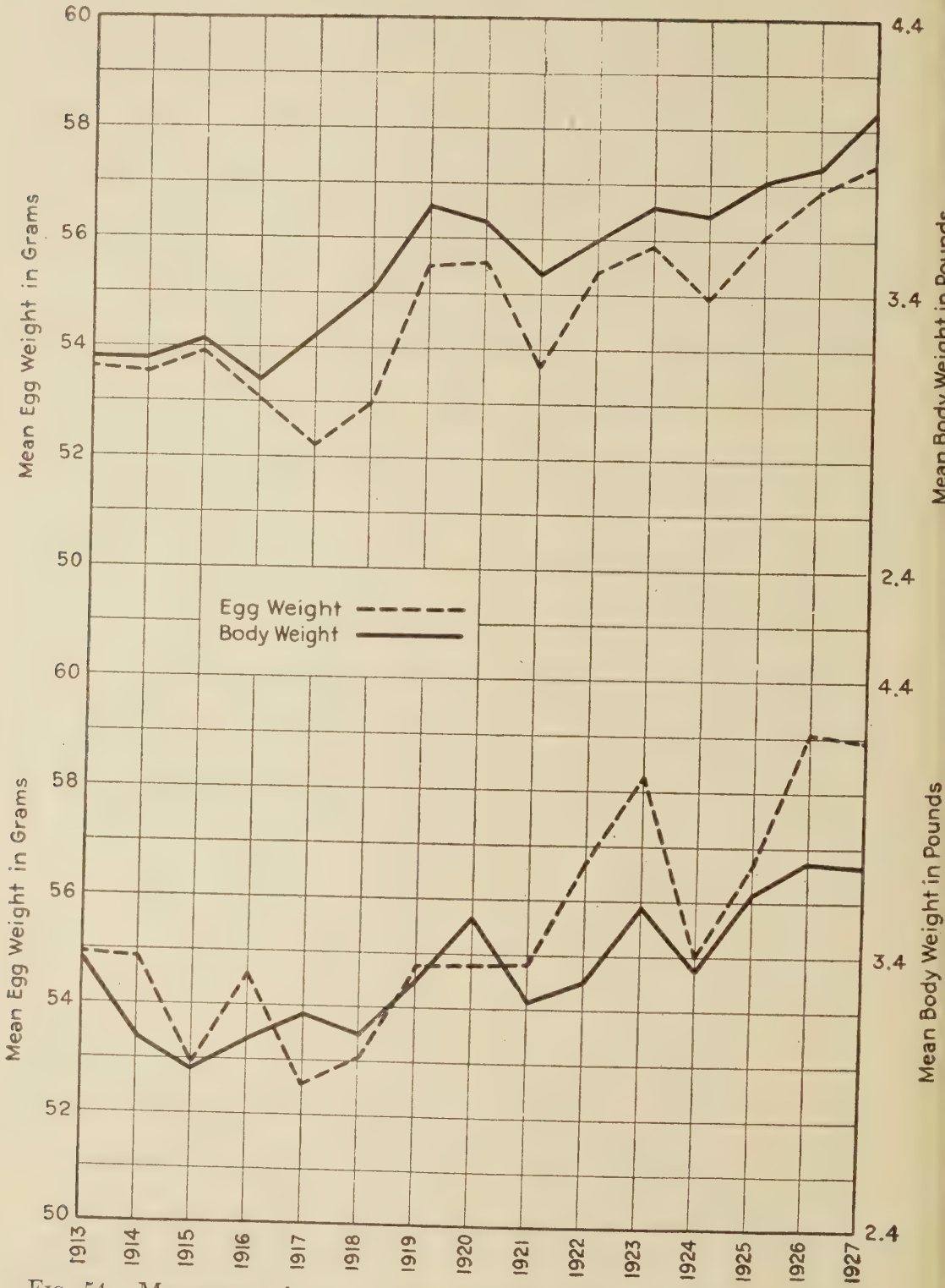

FIG. 54. Mean annual egg weight changed from year to year in accordance with changes in mean body weight in two strains of White Leghorns. (From data of Hall and Marble, 1930.)

concerning the relationship between the maximum body weight of the pullet and the mean egg weight of her annual production. Upp

nd Thompson (1927), with White Leghorns, corroborated Atwood's indings concerning the relationship between mean body weight and nean egg weight. Rhynehart (1929) observed that large birds tended o produce fewer second-grade eggs than smaller birds. For two trains of White Leghorns, Hauschildt (1929) gives correlations of 0.57 ± 0.05 and 0.72 ± 0.05, respectively, between body weight and nean egg weight.

In a group of 1,388 Rhode Island Reds, Hays (1930) observed that he birds which weighed most when they commenced laying laid the argest eggs up to the first of January, which terminated the period of observations.

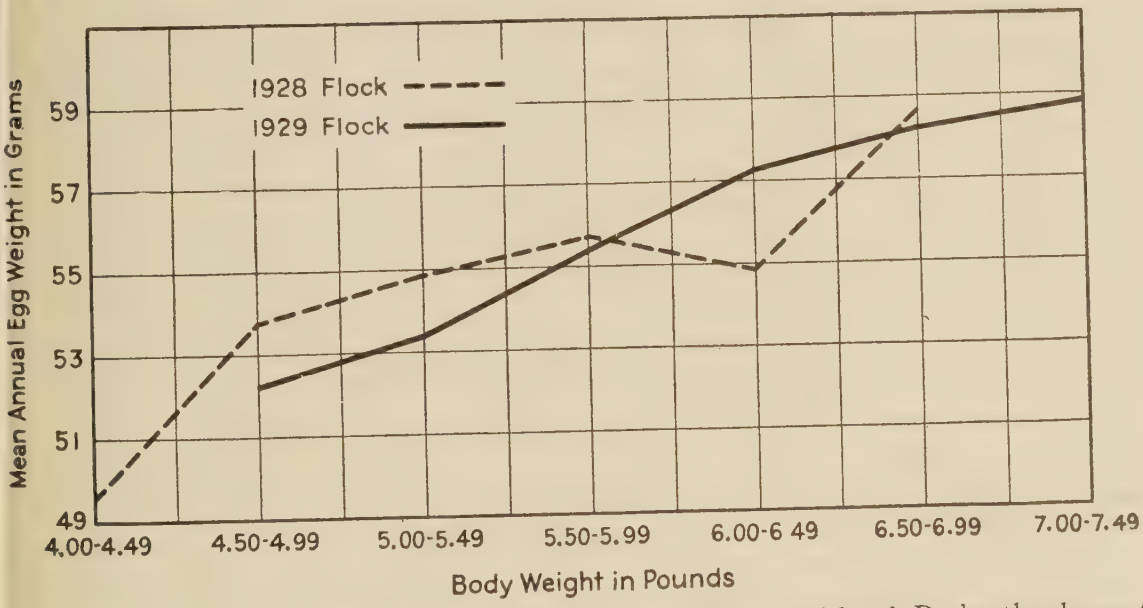

FIG. 55. In both the 1928 and the 1929 flocks of Rhode Island Reds, the largest birds laid the largest eggs. (From data of Graham, 1932.)

Atwood and Clark (1930) found that for Single-Comb White Leghorns in the first, second, and third years of production there was a significant positive correlation between body weight and the mean egg weight of the eggs produced by each bird. Marble (1930) observed a significant positive correlation between body weight and egg weight in six groups of White Leghorns and one group each of Barred Plymouth Rocks and Rhode Island Reds. Marble points out that the mean egg size increases as the body weight increases but at a diminishing rate. Upon attaining maximum body weight the relationship decreases.

Data regarding the relationship between body weight and egg weight in two strains of White Leghorns bred for 20 and 15 years, respectively, have been made available by Hall and Marble (1930). It was found that in general annual mean egg weight per bird followed the trend from year to year of mean body weight per bird: the larger

the bird the larger the egg, the situation being shown in graphic form in Fig. 54 for the years 1913 to 1927, inclusive.

Graham (1932) has shown that in the 1928 and the 1929 flock of Rhode Island Reds the smallest birds laid the smallest eggs and the largest birds the largest eggs. The data have already been given in Table 41 and the situation is shown graphically in Fig. 55. Knox (1933) and others have observed a significant positive correlation between average body weight and average annual egg weight among unselected stocks.

The relationship between egg weight for different periods and body weight is well illustrated by the data given in Table 49.

TABLE 49. AVERAGE WEIGHT OF EGGS, IN GRAMS, FOR DIFFERENT PERIODS IN RELATION TO AVERAGE BODY WEIGHT, IN POUNDS, IN WHITE PLYMOUTH ROCKS

(Funk and Kempster, 1934)

Average Body Weight	Number of Birds	Average Weight First 10 Eggs	Average Egg Weight Oct.–June	Maximum Monthly Egg Weight
3.6 to 4.5.....	10	49.3	52.7	54.5
4.6 to 5.5.....	65	52.2	55.4	57.0
5.6 to 6.5.....	40	54.5	56.8	58.9
6.6 to 7.5.....	7	56.7	58.7	60.7

The data in Table 49 show clearly that in these White Plymouth Rocks the largest birds laid the largest eggs at commencement of laying and throughout the year and that their maximum monthly egg weight was higher than that of the smaller birds.

Egg Weight in Relation to Sexual Maturity. Curtis (1914*b*) was probably the first to observe that the size of the first eggs laid in the pullet year of production depends to some extent on the age of the birds and the time of the year that laying commences. Lippincott (1921) with White Leghorns, Atwood (1923) with White Leghorns, and Jull (1924*b*) with Barred Plymouth Rocks successively determined the existence of a very significant correlation between age in days laying commenced and the mean weight of the first ten eggs laid in the pullet year: the earlier laying commenced the smaller was the average weight of the first ten eggs.

The increase in the mean monthly egg weight expressed as a percentage of the annual mean egg weight is shown in Fig. 56 for four groups of 40 Barred Plymouth Rocks, one group of which commenced

laying in September, one in October, one in November, and the other in December. The graph shows clearly that the earlier laying commenced the smaller was the size of the egg in relation to annual mean egg weight up to the month of February, at which time all four groups reached the vernal maximum in mean monthly egg weight.

The observations of Parkhurst (1926), Maw and Maw (1928), Hays (1930), and Schmidt and Zollner (1930) also tend to show that

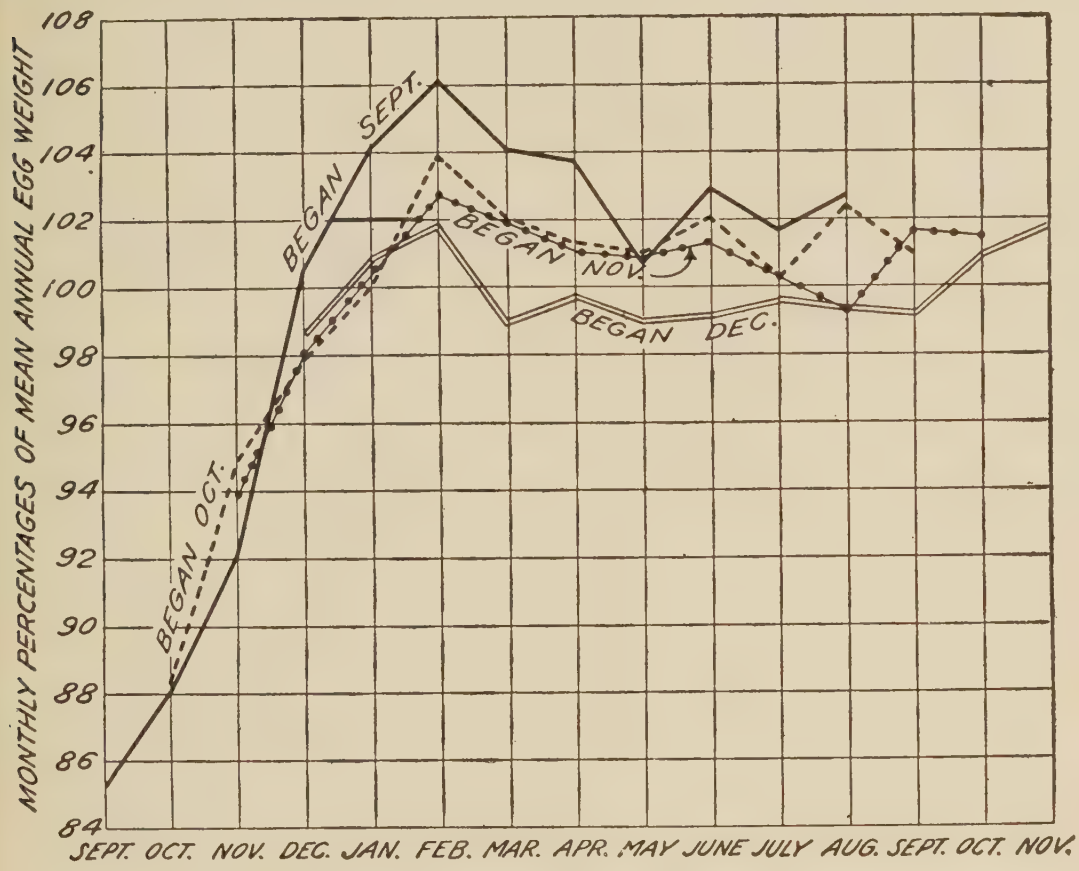

FIG. 56. Monthly mean egg weights as percentages of the mean weights of the annual production, in Barred Plymouth Rocks, according to the month laying commenced. The earlier in life that laying commenced the smaller were the first eggs laid. Regardless of the month that laying commenced, maximum egg weight was attained in February of the first laying year. (Jull, 1930.)

the earlier in life that laying commences the smaller is the weight of the eggs laid at that time. Just what effect this has on annual mean egg weight is discussed later in connection with the problem of the mean egg weight of the first-year production. In the meantime, it may be observed that Marble (1931) has stated that age in days that laying commences is not an important factor in determining mean egg weight of the first-year production. It should be kept in mind, however, that age at commencement of laying has a direct bearing on mean annual production, as pointed out in the previous chapter, and that undoubtedly the earlier in life that laying commences the less the average bird

weighs; consequently, since body weight has a direct bearing on egg weight, as pointed out previously, age in days that laying commences may be of greater importance in relation to mean annual egg weight than has been generally recognized.

Maw and Maw (1932) observed, from observations on egg weights in a flock of White Leghorns, that those birds whose first 10 eggs average less than 47.5 grams are not apt to lay eggs throughout the year that average standard weight. Jull and Godfrey (1933) obtained high correlations between the mean weight of the first 10 eggs and the annual mean egg weight and concluded that the latter was caused to a considerable extent by the factors responsible for the mean size of the first 10 eggs.

In White Leghorns and Barred Plymouth Rocks, Callenbach (1934) observed a significant positive correlation between age at sexual maturity and the weight of the first egg.

The relationship between the weight of eggs for different periods and sexual maturity is shown in Table 50.

TABLE 50. AVERAGE WEIGHT OF EGGS, IN GRAMS, FOR DIFFERENT PERIODS IN RELATION TO SEXUAL MATURITY IN DAYS, IN WHITE PLYMOUTH ROCKS

(Funk and Kempster, 1934)

Sexual Maturity in Days	Number of Birds	Average Weight First 10 Eggs	Average Egg Weight for Year	Maximum Monthly Egg Weight
151–200	23	49.1	54.9	57.5
201–225	32	50.8	54.9	57.4
226–250	41	55.0	56.8	58.7
253–325	26	55.9	56.8	58.4

The data in Table 50 show that the White Plymouth Rocks which commenced laying at 225 days or earlier laid relatively smaller eggs both for the first 10 eggs and throughout the year than birds commencing to lay at 226 days or later. Also, the maximum monthly egg weight of the group of earlier maturing birds was lower than that of the later maturing birds.

The relationship between the weight of eggs for different periods and body weight at sexual maturity is shown in Table 51.

The data in Table 51 show that the smaller the size of the bird when laying commences the smaller are the eggs laid at that time and throughout the year. Moreover, the maximum monthly egg weight

TABLE 51. AVERAGE WEIGHT OF EGGS, IN GRAMS, FOR DIFFERENT PERIODS IN RELATION TO BODY WEIGHT, IN POUNDS, IN WHITE PLYMOUTH ROCKS

(Funk and Kempster, 1934)

Body Weight at Sexual Maturity	Number of Birds	Average Weight First 10 Eggs	Average Egg Weight Oct.–June	Maximum Monthly Egg Weight
3.6 to 4.5.....	21	47.8	54.9	56.8
4.6 to 5.5.....	44	52.4	55.2	57.5
5.6 to 6.5.....	49	54.8	56.6	58.4
6.6 to 7.5.....	8	58.3	59.7	61.2

was directly related to body weight at sexual maturity in these White Plymouth Rocks.

The general conclusions to be drawn from this discussion on egg weight in relation to sexual maturity are that the earlier in life that laying commences the smaller the size of the bird, on the average, and the smaller the size of the egg, on the average. This situation is quite in keeping with the observation of Asmundson (1933) to the effect that, aside from the environment, the two principal factors determining the amount of albumen secreted by the oviduct include the size of the yolk and the size of the oviduct, both of which tend to increase approximately until the bird attains body maturity.

Among White Plymouth Rock pullets that commenced laying in October and November, Funk and Kempster (1934) observed that egg weight increased from the first egg laid to about the thirtieth egg.

In Rhode Island Reds, Hays (1934) found that within a genetically early-maturing population, extreme earliness of sexual maturity tended to increase greatly the length of time required for the attainment of standard egg weight. It was also found that small body weight at the first egg tended to increase the time interval for the attainment of standard egg weight.

In White Leghorns, Rhode Island Reds, and Barred Plymouth Rocks, Wilson and Warren (1934) concluded that the first few eggs laid should weigh at least the following specified grams, depending upon the month in which laying commenced: October or earlier, 46; November, 50; December or later, 52. Waters (1937), with White Leghorns, concluded that maximum egg weight is attained when a bird reaches maximum adult body weight, which he found to be at approximately ten months of age.

Egg Weight in Relation to Position of Egg in the Clutch. Atwood (1917) and Jull (1924*b*) have shown that the second egg of a two-egg clutch is usually smaller than the first egg. Atwood further found that, in clutches of several eggs, the first egg is usually the heaviest and that there is a progressive decrease in the weight of the

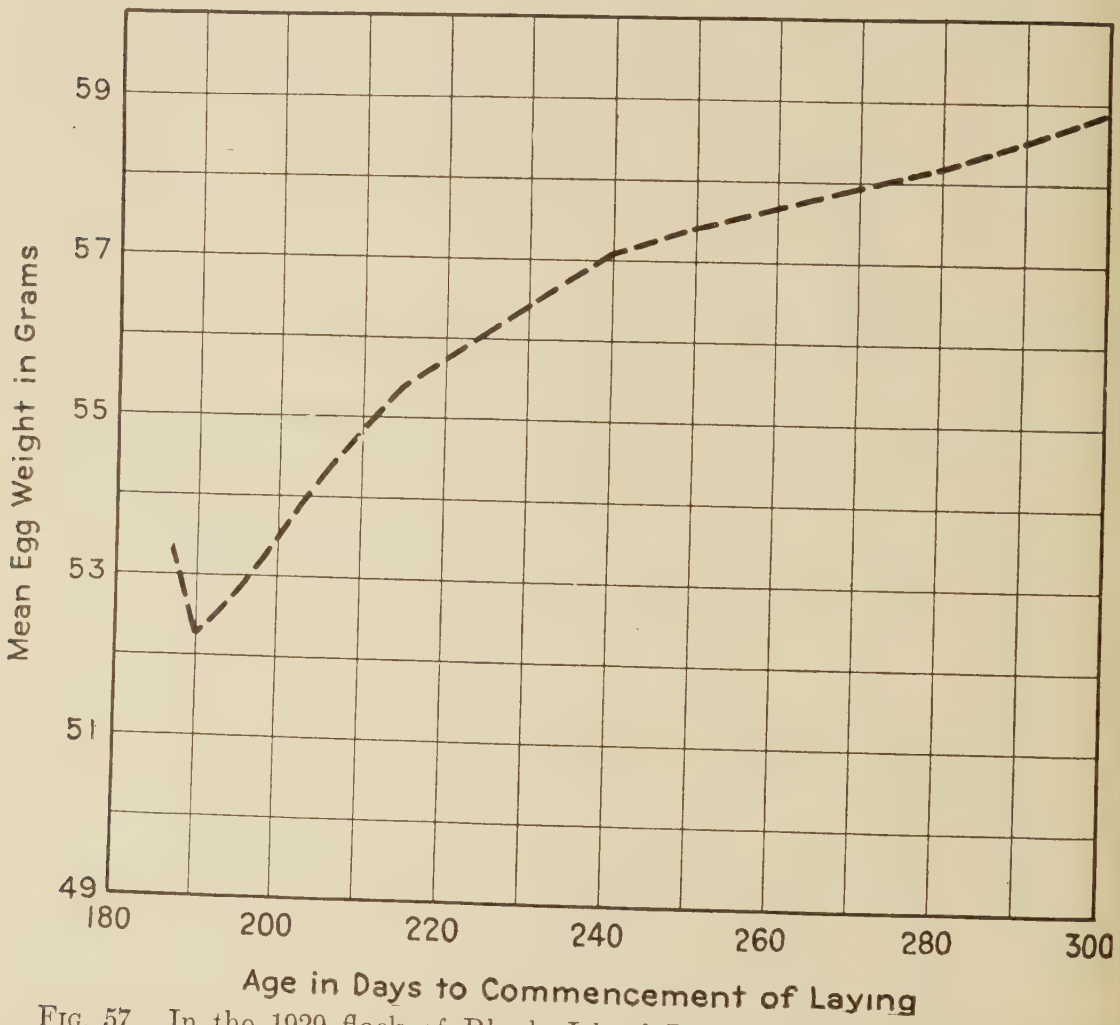

FIG. 57. In the 1929 flock of Rhode Island Reds it was found that the first year mean egg weight was relatively the lowest among the birds that started laying the earliest in life. (From data of Graham, 1932.)

egg laid on each successive day. However, the rate of decrease in the weight of the successive eggs in a clutch is less when birds are laying heavily than when they are not laying heavily, according to Atwood (1926). This observation has been confirmed by Funk and Kempster (1934).

Egg Weight in Relation to Rate of Laying. Birds that lay at the highest rate or greatest intensity are frequently birds that lay small-sized eggs. In a group of 1,392 Rhode Island Red pullets, Hays (1930*a*) obtained a negative correlation of -0.32 ± 0.02 between rate of egg production and mean egg weight to the first of

January. The value of this correlation indicates that birds that lay at the fastest rate are inclined to be those that lay the smallest eggs, or those that lay the smallest eggs are inclined to lay at the fastest rate.

Hays (1934) further observed that a very high rate of laying during the winter months increased the length of time required for a bird's eggs to attain standard weight as compared with a low winter rate of laying.

Mean Egg Weight of the First-Year Production. During the first-year production in a group of White Leghorns, Atwood (1914) found that egg weight varied from month to month and reached the maximum in the early spring. Hadley (1919) developed the thesis that increase in egg weight from the time the pullet commences laying serves as a criterion of numerical production and that it is possible to determine in advance of the conclusion of the first year of production the relative potential laying capacity among individuals in a flock of pullets. In connection with Hadley's thesis, Jull (1925) has pointed out that increase in egg weight can be considered a criterion of numerical production only so far as age in days at the time that laying commences is a criterion of numerical production.

The relationship between the mean egg weight and the number of eggs laid during the first laying year has been studied by Atwood (1923), Jull (1924*b*, 1925), Lohman (1924), Parkhurst (1926, 1927), Upp and Thompson (1927), Thompson (1930), Atwood and Clark (1930*a*), and Dudley (1931), the results of all these investigations showing that the mean egg weight of the annual production is not affected by the number of eggs laid.

On the other hand, Hays (1929) found that heavy winter production, in Rhode Island Reds at the Massachusetts Experiment Station, tended to be accompanied by small egg size. Atwood and Clark (1930*b*) found that in a flock of 200 unselected White Leghorns there was a tendency for the best layers to lay the smallest eggs. A significant negative correlation of -0.22 ± 0.06 between egg production and mean egg size per bird was determined for those birds which laid 170 eggs or more in the first year of production. Evidence showing that the best layers tend to lay small eggs as compared with birds that do not lay so well is available from a number of other sources.

White Leghorns, Rhode Island Reds, and White Wyandottes, in a Scottish laying contest conducted by the Department of Agriculture for Scotland, were divided into two groups according to the mean weight of egg laid. The mean egg size and the mean production for each group were determined by Jull (1930), who found that the

highest producing hens laid the smallest eggs. Jull (1930) analyzed the records of 185 White Leghorns in the English National Poultry Council trials and found that there was a tendency for the highest producers to lay the smallest eggs. Jull (1930) also analyzed the records of egg production for eleven months in a group of 40 White Leghorns at the West Virginia Experiment Station and determined a correlation of -0.39 ± 0.12 between mean egg production and mean

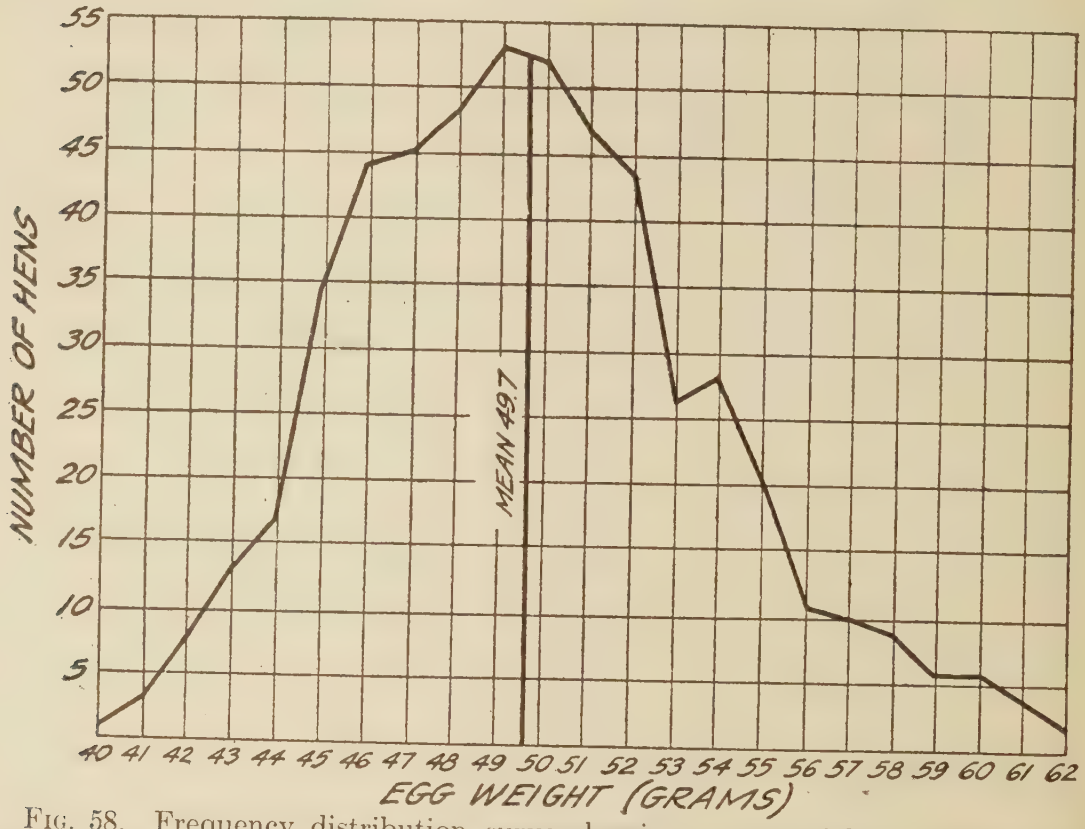

FIG. 58. Frequency distribution curve showing mean weight of eggs laid by 526 Rhode Island Reds from the date each pullet laid her first egg to January 1. (Hays, 1929.)

egg weight per bird. In this group of birds, therefore, the best layers were among those that laid the smallest eggs.

In a group of 74 White Leghorns hatched in March and April, Maw and Maw (1931) found that the annual mean egg weight was lowest for those birds that started to lay the earliest. They also found that the earlier in life laying commenced the longer was the time required for a bird to lay eggs of standard weight, 56.70 grams. Graham (1932) found that in a flock of 163 Rhode Island Reds hatched in 1929 at the Massachusetts Experiment Station, there was a progressive increase in annual mean egg weight as the age at commencement of laying increased. The data are given in Table 41 and are shown in graphic form in Fig. 57. Jull, Quinn, and Godfrey (1933)

found that in a group of 51 unselected White Leghorns, whose first-year production ranged from 20 to 283 eggs and whose mean annual egg weight per bird ranged from 49.80 to 61.67 grams, there was a marked tendency for the best layers to lay the smallest eggs.

From the foregoing discussion on the relationship between annual mean egg weight and first-year production, it is apparent that the observations of the various investigators are not in entire agreement, since some of them did not find a significant relationship, whereas others did. In this connection, Marble (1930) has observed that the relationship between mean egg weight and first-year production is nonlinear in nature, and that these two factors are correlated to a small degree when the relationship is measured by means of the correlation ratio.

Galpin (1937–1938) has produced evidence indicating that the decrease in egg weight that occurs during the spring and early summer months is related to the decrease in the functioning of the thyroid gland. He found that among White Leghorn hens the thyroid weight decreases from the time of the onset of reproductive activity till July and then increases, attaining maximum weight in October and November.

First-Year Egg Weight Determinations. The weighing of every egg laid by each of the members in a flock during the entire first year of production involves a tremendous amount of time and labor and is out of the question for the practical poultry breeder. But the poultry breeder and the investigator are both interested in determining the most logical method of selecting breeding stock on the basis of the size of eggs they lay in order that by the adoption of proper breeding methods strains can be developed which will be noted for the good size of the egg produced.

In most of the studies on the inheritance of egg weight which have been conducted, the average egg weight of the first-year production has been the measure used. The results of investigations have shown, however, that it is only necessary to weigh a relatively small number of the eggs laid by a bird in order to determine with a high degree of approximation the average weight of all eggs laid during the first-laying year.

Jull (1930) found that weighing the eggs laid on the same day each week throughout the first-laying year or weighing each of the first ten eggs laid in March was quite sufficient, the average weight of each group of eggs laid being nearly the same as the average egg weight of the first-year production.

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TABLE 52 THE AVERAGE WEIGHT IN GRAMS OF THE FIRST 10 EGGS LAID IN MARCH AND OF THE EGGS LAID ON THE SAME DAY EACH WEEK COMPARED WITH THE AVERAGE EGG WEIGHT OF THE ANNUAL PRODUCTION OF 21 WHITE LEGHORNS

(Jull, 1930)

Number of Bird	Average Weight of First 10 Eggs in March	Average Weight of Eggs Laid on One Day Each Week	Average Weight of Annual Production
5	52.16	53.08	52.52
11	50.91	51.77	51.33
14	50.18	51.95	52.45
16	59.52	61.45	61.96
24	51.46	54.17	53.71
27	49.58	50.13	50.29
35	55.08	54.31	54.36
36	56.47	57.12	57.45
40	50.40	50.67	50.36
41	52.39	52.96	53.16
44	48.81	49.67	50.02
45	53.44	52.21	52.18
51	48.06	50.18	49.95
52	56.11	59.86	59.14
53	49.27	50.46	50.75
54	57.09	57.48	58.07
64	51.87	54.89	54.36
67	52.63	52.22	52.40
71	56.94	56.86	56.33
74	54.07	54.68	54.63
77	49.99	50.09	49.61
	52.69	53.63	53.57

In the great majority of cases, the differences between the average weight of the first ten eggs laid in March and the average weight of the annual production are not significant, indicating that the average weight of the first ten eggs laid in March by the average member of a flock may be regarded as an index of the average egg weight of the annual production. In no case is the difference between the average weight of the eggs laid by a bird on a given day each week and the average egg weight of the annual production significant, indicating that a reliable index of average egg weight of the first-year production is obtained by weighing the eggs that are laid on a given day each week.

Dudley (1930–1931), in a group of 198 White Leghorns entered

in an English laying contest, found that weighing eggs laid on four consecutive days each month or one day a week served as a good index of the first-year average egg weight for each bird. Maw and Maw (1932), in a flock of 74 White Leghorns, found that the average weight of the first ten eggs laid by each bird in the fifth month of laying gave a reliable index of her first-year average egg weight. Godfrey (1933) concluded that weighing the eggs laid by each bird on the first four days of each month or on a given day of each week served as a reliable index of the first-year average egg weight, the latter method being more reliable than the former. Waters (1937) suggested that the proper time to obtain a measure of a bird's maximum egg weight is approximately at ten months of age, when mature body weight has presumably been attained. Jeffrey (1938) concluded that the average weight of the first ten eggs in March was a measure of first-year average egg weight superior to any measure taken before a bird reached body maturity.

Decline in Yearly Average Egg Weights. It has already been pointed out that during the first-laying year in most flocks there is an increase in size or weight of eggs laid from the time that laying commences up to the spring of the year. Maximum egg weight is usually attained in February or March; during the late spring and the summer there is often a slight relative decline, followed by an increase at the close of the first-laying year.

According to Hadley and Caldwell (1920), Benjamin (1920), Atwood (1926, 1928), Atwood and Clark (1930), Waters (1937), and Clark (1940) the average egg weight of the second-year production varies from about 4 to 8 per cent greater than that of the first year. Hens that lay small eggs the first year tend to lay eggs that are relatively small eggs the second year compared with hens that lay large eggs the first year. Apparently there is relatively little change in the yearly average egg weight from the second to the third and successive years of production.

The Genetics of Egg Weight. From what has already been said about the numerous factors affecting the weight of eggs laid, it is quite apparent that the problem of determining the nature of the inheritance of egg weight is an extremely complicated one. In the first place, it has never been determined whether the mean egg weight of the first-year production or the maximum weight of eggs that a bird lays during the first or any other year is the proper basis for determining the nature of the inheritance of egg weight. In the second place, since egg weight has been shown to be so closely associated with body weight, the problem of the inheritance of egg weight would seem

to be intimately related to the problem of the inheritance of body weight. In the third place, since it has been shown in the preceding chapter that usually the earlier in life that laying commences the greater the number of eggs laid, and since it has been shown in this chapter that the earlier in life that laying commences the smaller is the size of both body and egg at that time and the longer thereafter before either maximum body or egg weight is attained, the average weight of eggs laid during the first-laying year may perhaps be determined largely by controlling the age in days at which laying commences in relation to body weight. These are undoubtedly only a few of the problems involved in any study on the inheritance of egg weight.

Since the commercial egg-weight standard is 24 ounces per dozen or 56.7 grams per egg, it should be the desire of every poultry breeder and commercial flock owner to breed and keep only those birds that lay eggs of approximately these weights. However, if a pullet lays eggs approximating 2 ounces or 56.7 grams each in weight when she commences laying she will most probably lay larger eggs in the spring of the year when eggs are incubated and still larger eggs in the second year.

Maw and Maw (1932), in a flock of White Leghorns whose average egg weight was 53.73 grams, found that only when the first ten eggs laid by each pullet averaged 47.50 grams were eggs of standard weight laid before the end of the first year of production. Hays (1937), in Rhode Island Reds, found that birds whose egg production to January first averaged less than 53 grams per egg rarely laid eggs averaging at least 56.7 grams per egg in February or March. Waters (1937) suggested using egg weights obtained at approximately ten months of age as the proper basis for studying the inheritance of egg weight. Jeffrey (1938) made a similar suggestion in concluding that the average weight of the first ten eggs in March should be the basis of inheritance studies.

Comparatively few experiments have been conducted for the purpose of determining the specific nature of the inheritance of egg size or weight. The problem is an extremely complicated one, for the simple reason that the following factors, among others, have been found to influence egg weight: the size of the bird in a given strain, the size of the yolk, the size of the oviduct, sexual maturity, high temperatures, and perhaps one or more of the hormones secreted by some of the endocrine glands.

Results secured indicating that small egg size is dominant to large egg size were reported by Hurst (1921) and Kopeć (1924). On the other hand, results secured indicating that large egg size is dominant

o small egg size were reported by Benjamin (1920), Waters and Weldin (1929), and Hays (1929, 1937). No definite conclusions are possible at this time.

That it is possible to develop strains laying characteristically small-ized eggs as well as strains laying characteristically large-sized eggs has been demonstrated by Waters and Weldin (1929). By careful election, they developed one strain which during the last five years of breeding laid eggs whose average first-year weight per bird approxi-mated 48 grams, whereas another strain during the last six years of breeding laid eggs whose average first-year weight per bird approxi-mated 60 grams. They came to the conclusion that the male and the female have an equal influence in transmitting egg size. Evidence secured from matings made between the two strains suggested the possi-bility that large egg size is due to a dominant autosomal gene, although probably other genes also play a part.

Using the average weight of eggs per bird from the commencement of laying to January first of the first-laying year, Hays (1929, 1937) concluded that the inheritance of egg size depends upon three domi-nant autosomal genes, *A*, *B*, and *C*. Gene *A* is said to be epistatic to genes *B* and *C* and produces small eggs. Either gene *B* or *C* is said to produce eggs of standard weight during the normal hatching season, and when they are present together they exercise a cumulative effect in producing eggs of very large size. This interesting theory of the inheritance of egg size needs to be substantiated by backcross and F_2 matings of strains differing significantly in egg weight before it can be concluded that so relatively few genes are involved. Particularly is this so, inasmuch as it has already been shown that so many physio-logical factors, such as sexual maturity and body weight, influence egg size, the inheritance of each of the physiological characters being determined by a relatively large number of genes. In addition, Munro (1938) has submitted evidence which indicates that yolk weight is a heritable characteristic. It seems safe to conclude, therefore, that many genes are responsible for determining egg weight.

Olsen and Knox (1940) have presented the data in Table 53, indicating the possibility of increasing the average egg weights of succeeding generations of pullets by means of the progeny-test method of selecting the breeding stock. Not only was there an increase in the average egg weight of the annual production of each succeeding generation of pullets but the month during which eggs of standard weight were first attained was advanced each year during the five-year project.

TABLE 53. INCREASE OF EGG WEIGHT IN FIVE YEARS' BREEDING OF WHITE LEGHORNS

(Olsen and Knox, 1940)

Year	Average Yearly Weight		First Month Standard or Maximum Weight Was Attained		
	Grams per Egg	Ounces per Dozen	Month	Grams per Egg	Ounces per Dozen
1934–1935....	54.7	23.2	May	56.0	23.7
1935–1936....	55.7	23.6	March	56.7	24.0
1936–1937....	56.8	24.0	February	56.7	24.0
1937–1938....	58.5	24.8	January	57.4	24.3
1938–1939....	59.7	25.3	December	56.8	24.0

Olsen and Knox concluded, from an analysis of their data, that sire and dam contribute approximately equally to the inheritance of egg weight.

THE INHERITANCE OF EGG SHAPE

The problem of the inheritance of egg shape has its practical significance because all the eggs marketed from a flock should be of approximately the same shape in order to avoid breakage when shipped in cartons or cases and in order to present the most attractive appearance to the buying public. Uniformity of shape, therefore, is of considerable practical importance. Investigational work has shown, however, that, although most birds in a flock usually lay eggs that are characteristically uniform in shape, some hens lay eggs that are quite variable in shape. The poultry breeder should attempt to ascertain those birds which lay eggs lacking in uniformity, as well as those birds which produce other birds that lay eggs lacking in uniformity, and eliminate them from his flock.

The normal shape of a hen's egg is ovate, with one end larger and relatively more blunt than the other end. In order to compare eggs in regard to their shape, they are measured and a shape index determined. The method of determining egg shape most commonly employed is the length-breadth index, which is found by multiplying the breadth by 100 and dividing the product by the length. This was the method employed by Pearl and Surface (1914) and Curtis (1914*b*) in their extensive investigations on variability of egg shape. R. and A.

Serebrovsky (1926), however, used the measurement of length and two breadth measurements, the latter being taken a certain distance from each end of the egg. Asmundson (1931*a*) used the length measurement and four breadth measurements approximately the same distance apart, thus taking into consideration differences in the diameter near the ends of the eggs.

Factors that apparently operate in producing the characteristic ovate shape have been studied by a few investigators whose views differ slightly. Ryder (1893) concluded that the shape of the egg was due to the resistance of the oviduct in front of the egg as it passed down the oviduct and to pressure behind the egg. Cushny (1902) observed that the muscular layer of the uterus was thicker than other regions so that the uterus apparently exercised the greatest influence in producing the shape of the egg. Szielasko (1905) suggested that the uterus gave the egg its definite form, whereas D'Arcy Thompson (1908) felt that the ovate shape was due largely to the nature of the pressure exerted by the oviduct, the pressure being greatest behind the middle of the egg, owing to the nature and direction of the peristaltic action of the oviduct.

After a careful study of the problem, Pearl (1909) came to the conclusion that, although the general shape of the egg may be determined before it reaches the uterus, the particular form of each egg is determined by the muscular activity of the walls of the uterus. Curtis (1914*b*), however, concluded that the muscular activity of the oviduct was primarily responsible for the shape of the egg. R. and A. Serebrovsky (1926) state that not only the muscular activity but also the shape of the oviduct is a factor in determining the shape of the egg.

The problem of the variation in the shape of eggs has been investigated extensively by Asmundson (1931*a*), who performed operations on the oviduct and on the uterus to determine the effect on the shape of the egg. Altering the shape of either the isthmus or the uterus of the oviduct affected the shape of the eggs laid subsequent to the operation, but the effect in some cases was not apparent, owing, Asmundson was led to believe, to the muscular activity of the oviduct. Asmundson concluded that there are three factors that determine the general shape of an egg: first, the amount of albumen secreted in the albumen-secreting portion of the oviduct; second, the size of the lumen of the isthmus and the albumen-secreting portion of the oviduct; third, the muscular activity of the walls of the isthmus and the albumen-secreting portion of the oviduct. It was further concluded that the general shape may be more or less altered in the uterus, which, together with the isthmus, gives each egg its particular shape.

The inheritance of egg shape has been investigated to a slight extent only. Benjamin (1920) observed that egg shape is inherited and that long, narrow eggs apparently are dominant to short, round ones, whereas Kopeć (1924) observed the reverse, but neither investigator made any determinations of the number of genes involved. Whether egg shape is inherited in Mendelian manner remains to be determined by carefully controlled experiments, Klodnits Kii (1935) having supplied evidence that egg shape is a hereditary characteristic, although Hays (1937) was unable to demonstrate that the egg shape is inherited.

THE INHERITANCE OF EGG-SHELL COLOR

Certain breeds lay brown-shelled eggs and other breeds lay white-shelled eggs; it is very desirable for a flock in the first group to produce eggs of a uniform shade of brown and for a flock in the second group to produce eggs that are completely free from tints, an objection sometimes encountered in Leghorn, Ancona, and other breeds that normally lay white-shelled eggs. The Araucana breed from South America lays an egg with a blue-tinted shell.

In brown-shelled eggs, the color is due to one type of pigment, the principal representative of which is oöphorin, according to Fischer and Kogl (1921, 1923). The blue color of the shell of the egg of the Araucana is reported by Punnett (1933) to be due to banded oöcyan. Although each hen lays eggs whose shells are approximately the same shade, the degree of pigmentation is influenced by production. In fact, Benjamin (1920) found greater variability in the color of the shell than in the size and shape of eggs laid by the same hen. Benjamin states that "Each year there is a tendency for the eggs produced to become gradually whiter during the first five or six months of production, and then to become more tinted again toward the end of the production season." On the other hand, Kopeć (1927*a*) observed that the intensity of coloring decreased as production increased. The statement by Benjamin may be reconciled with the observation of Kopeć by assuming that in Benjamin's birds there was a decrease in the rate of laying after the first five or six months.

Kopeć also observed that short, round eggs tend to be more deeply pigmented than elongated eggs because the short, round eggs tend to remain for a longer time in the uterus, where the shell is colored. In this connection, Giersberg (1923) concluded that the pigmentation of the shell is completed in the uterus, whereas Asmundson (1931*a*) found that the isthmus portion of the oviduct influences the pigmentation of the shell. It seems highly probable, therefore, that both the isthmus

and uterus portions of the oviduct are responsible for the pigmentation of the shell of the egg, most of the pigment being secreted in the uterus.

The problem of the inheritance of egg-shell color is important from the standpoint of having a flock representing a brown-shelled breed lay eggs of a uniform brown color, but is still more important from the standpoint of eliminating birds that lay tinted eggs in a flock representing a white-shelled breed.

Taylor and Lerner (1938) observed that some of their White Leghorns laid eggs having a glossy shell and that when these birds were crossed with White Leghorns that laid eggs having chalk-white shells, the chalk-white characteristic proved to be dominant.

Hurst (1905) and Benjamin (1920) observed that the F_1 progeny produced by crosses between white-shelled and brown-shelled breeds laid eggs of an intermediate tint.

The most extensive investigation of the inheritance of egg-shell color is that by Punnett and Bailey (1920), a good summary of the results they secured being given by Punnett (1923). The conclusion arrived at was that the difference between breeds that lay white-shelled eggs and breeds that lay brown-shelled eggs is due to one gene of major importance and several genes of minor importance.

Birds in which the gene of major importance is absent and the multiple genes of minor importance are also absent lay white-shelled eggs. Birds in which the gene of major importance is absent but one or more of the multiple genes of minor importance is present lay lightly tinted eggs, the degree of tint depending upon the number of multiple genes of minor importance present. Birds in which the gene of major importance is present lay dark-tinted-shelled eggs, the degree of tint depending upon the number of multiple genes of minor importance present. Birds in which the gene of major importance is in a homozygous condition lay eggs whose shells are dark brown in color. Punnett has also suggested that some strains that normally lay white-shelled eggs carry a gene that inhibits the development of pigmentation in eggs.

Kopeć (1927*b*) secured slightly different results from those of Punnett and Bailey and came to the conclusion that his white-shelled and brown-shelled egg breeds differed in several genes determining egg-shell color, all genes apparently being of equal importance. Axelsson (1932), in crossing White Leghorns with Rhode Island Reds or Barnevelders, a Dutch breed which lays a dark-brown egg, concluded that egg-shell color is sex-linked. In studying egg-shell color inheritance in Rhode Island Reds, Hays (1937) concluded that multiple genes are involved. It has been found that when the Araucana is

crossed with a white-egg or a brown-egg breed the eggs laid by the crossbred progeny are blue tinted, showing that blue is incompletely dominant to nonblue.

Apparently the only definite conclusion that can be drawn from the results secured in the studies on the inheritance of egg-shell color is that neither the white-shelled nor the brown-shelled character is dominant and that there are probably several genes that determine dark-brown pigmentation. From the practical standpoint it is obvious that poultrymen who breed Leghorns or other breeds laying white-shelled eggs should exercise the greatest care in eliminating all tinted-shelled eggs from among those to be incubated; also the birds that lay tinted-shelled eggs should be eliminated from the breeding flocks, and males from hens that lay tinted-shelled eggs should never be used as breeders.

Does Xenia Occur? The phenomenon known as xenia refers to the supposed change in the shell-color of the eggs laid by a female after being mated to a male representing a breed which lays eggs of a different shell color from that of the breed to which the female belongs. For instance, if a Leghorn female, which normally lays white-shelled eggs, after being mated to a Plymouth Rock male lays tinted-shelled eggs, or if a Rhode Island Red female, normally laying dark brown-shelled eggs, after being mated to a Minorca male lays eggs the shells of which are lightly tinted, the phenomenon of xenia is said to occur. The semen of the male is supposed to affect the normal shell color of the eggs laid by the female.

Among the various reported instances of xenia the more noteworthy seem to be those of Holdefleiss (1911), v. Tschermak (1915), and Kopeć (1922). Holdefleiss claimed that Plymouth Rock females laid eggs with more lightly tinted shells after being mated to Leghorn males. v. Tschermak mated a Langshan male to a White Leghorn female, a Plymouth Rock male to a Brown Leghorn female, and a Cochin male to a White Minorca female, and claimed that there was a darkening of shell color in the eggs laid after each mating was made. Three reciprocal matings were made, and in each case v. Tschermak claimed that the shells of the eggs laid became lighter in color after mating took place. Kopeć observed that after Polish Greenleg females were mated to a Leghorn male they laid eggs the shells of which were lighter in color than their eggs of the previous year.

All these cases and others in which xenia is supposed to have occurred have been examined thoroughly by Kopeć (1926), who has shown that in every instance the results are inconclusive either because of the small number of birds involved or because of the small

number of eggs on which the observations were based or because the various investigators failed to take into consideration the natural changes occurring in the pigmentation of the shell in relation to production. Walther (1914) claimed that the observations of Holdefleiss were entirely groundless. Kopeć criticized v. Tschermak's observations on the grounds that no "control" birds were observed, and Kopeć has pointed out that in connection with his own earlier observation of the supposed occurrence of xenia he had overlooked the periodical changes in shell color that usually take place.

The matter was investigated by Kopeć (1927*a*, 1927*b*) in reciprocal matings between White Leghorns and Buff Orpingtons, and "control" birds were also kept under observation. In addition, the results were carefully recorded for eggs laid by White Leghorn females into which were injected pieces of Buff Orpington testicles and for eggs laid by Buff Orpington females into which were injected pieces of White Leghorn testicles. Kopeć came to the conclusion that xenia does not occur in the domestic fowl, this being confirmed by Axelsson (1932).

THE INHERITANCE OF EGG-SHELL THICKNESS

The relative thickness of egg shells is an important factor in preventing breakage in the commercial transportation of eggs, particularly with respect to modern methods of packaging eggs. Willard and Shaw (1909) submitted evidence indicating that individual hens differ with respect to the percentage of egg shell of total egg weight and Romanoff (1929), Morgan (1932), Stewart (1936), and Lund, Heiman, and Wilhelm (1938) showed that egg-shell thickness or breaking strength is highly correlated with breaking strength. Romanoff (1929) also showed that individuals differ with respect to the breaking strength of their egg shells.

Evidence indicating that hens differ with respect to their ability to produce eggs differing in shell strength was submitted by Taylor and Martin (1928), their Barred Plymouth Rock eggs being significantly lower in percentage of shell than their White Leghorn eggs. Data obtained by Morgan, Mitchell, and Roderick (1931) and by Morgan (1932) showed that their strains of White Leghorns and Barred Plymouth Rocks differed significantly with respect to the percentage of egg shell and breaking strength. Van Wagenen, Hall, and Wilgus (1937) also showed that the eggs of their Barred Plymouth Rocks had a lower breaking point of egg shell than the eggs of White Leghorns, New Hampshires, and Rhode Island Reds. On the other hand, Baskett, Dryden, and Hale (1937) observed no difference among White Leghorns, White Wyandottes, and Rhode Island Reds with respect to the

breaking strength of egg shells, but it was observed that within each breed the individuality of the hen was the most important factor in determining the breaking strength of egg shells.

Munro (1938), in a Barred Plymouth Rock flock of 180 birds has shown that the progeny of different dams differed more with respect to the percentage ash of the dry shell and the percentage ash of the total egg than did the progeny of individual dams. The genes concerned with calcium utilization, it has been suggested, produce their effect by regulating the efficiency of the absorption, the mobilization in the tissues, and the secretion in the form of shell, of a given calcium intake.

Taylor and Lerner (1939), on the basis of the phenotypic selection of White Leghorn females mated to related males, succeeded in developing two lines that differed significantly with respect to the amount, thickness, and percentage of egg shell. The project was carried on for four generations, the results secured indicating that the egg-shell character of the dam was of major importance in determining the shell thickness of the eggs of her progeny. At the same time, it is postulated that "although in this work it seemed to produce lines with significantly different percentages of shell, further generations of the same type of selection gave no greater differentiation between the lines or any apparent increase in homozygosity, which would be shown by decreased variability of the expression of the character." It was suggested that the selection of potential breeding females for relatively high percentage of egg shell during the winter months of the first-year production seemed to be practical.

It was found, however, that the line of White Leghorns exhibiting relatively high percentage of thick egg shells differed from the line exhibiting relatively low percentage of thick egg shells with respect to the percentage of egg shell in the second egg of a clutch, the high line exhibiting less difference between the first and second eggs of a clutch than the low line. The females of the thick-shelled line maintained the ability to produce eggs with relatively little or no decrease in the percentage of thick shell from the first and second clutch positions, but the pullets from the thin-shelled line showed a greater tendency to produce eggs in which the shell percentage of clutch-two egg was lower than in clutch-one egg. It was finally concluded that, in view of the fact, as demonstrated by Morgan and Mitchell (1938), that there are individual differences between birds with respect to their ability to maintain a positive calcium balance and an efficient output of calcium as egg shell, there exists the possibility that hens which show a relatively great decrease in the amount and proportion

of egg shell with successive eggs of a clutch might be in some way inefficient in calcium metabolism.

INHERITANCE OF INTERIOR QUALITY

Since it has been demonstrated that egg production, egg weight, and thickness of shell are inherited, it seems reasonable to suppose that the quality of the interior of the egg is also inherited. The color of the yolk and the proportion of thick and thin white are regarded as indexes of quality. Concerning the former, about all that can be said at present is that yolk color is influenced markedly by the kind of diet fed, xanthophyll-bearing feeds such as greens and yellow corn producing a deep yellow yolk, whereas a diet containing no greens or yellow corn but much wheat and white corn produces a pale yellow yolk. At the same time, it has been observed that among birds fed the same diet there are individual differences concerning their ability to utilize and deposit yellow pigment in the yolk.

Breed and Interior Quality. The possibility of breeds differing with respect to the interior quality of their eggs was investigated by Van Wagenen, Hull, and Wilgus (1937), who showed that Barred and White Plymouth Rock eggs were significantly poorer in the condition of firm albumen than White Leghorn, New Hampshire, and Rhode Island Red eggs. In the percentage of firm white, the American breeds exhibited no greater variability between pens than within pens, whereas the White Leghorns exhibited greater variability between pens than within pens, indicating strain differences with respect to this character.

Knox and Godfrey (1934) observed that their White Leghorns laid eggs having a significantly higher percentage of thick white than their Rhode Island Reds, but they also stated that "the range of percentage of thick white is greater within the breed than between breeds." Wilcke (1936) observed that eggs from individual inbred hens were more uniform with respect to the combined viscosity of the entire contents of the egg than were eggs from noninbred hens.

Inheritance of Percentage of Thick White. The fact that the percentage of thick white in total white is an inherited characteristic has been demonstrated by different investigators, although the nature of the inheritance has not been determined. Holst and Almquist (1931) were among the first to show that the percentage of thick white is a characteristic dependent upon the individual hen. This was confirmed by Wilhelm and Heiman (1936). Lorenz, Taylor, and Almquist (1934) succeeded in establishing by selection two lines of White Leghorns that differed significantly with respect to the percentage of thick white in their eggs. The results secured indicated that genes

control to some extent the percentage of thick white formed and that possibly genes determining low percentage of thick white are dominant to genes determining high percentage of thick white.

Although Knox and Godfrey (1934) observed that their White Leghorns laid eggs having a significantly higher percentage of thick white than their Rhode Island Reds, in neither breed was the percentage of thick white significantly correlated with egg weight or with antecedent egg production. Lorenz and Almquist (1936) found that the percentage of thick white is lowered by high temperatures immediately after the egg is laid but is not affected by egg weight.

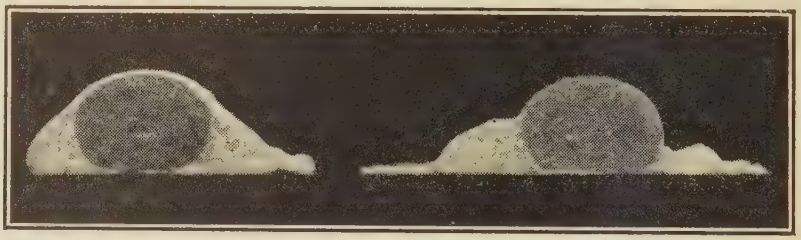

FIG. 59. Showing the marked difference in the appearance of thick white surrounding the yolk. The egg on the left is from a strain of birds that lay eggs in which the thick white is about 65 per cent of the total white. The egg on the right is from a strain of birds that lay eggs in which the thick white is about 45 per cent of the total white. (Knox and Godfrey, 1940.)

Van Wagenen and Hall (1936) made observations on six measures of interior egg quality for evidence of inheritance and found that the score of the condition of thick white is apparently inherited.

Van Wagenen, Hall, and Wilgus (1937) observed that percentage of thick white was not related to egg production in several different breeds and that the different breeds did not differ among themselves with respect to the percentage of thick white. Munro (1938), in Barred Plymouth Rocks, came to the conclusion that environmental factors are largely responsible for much of the variability in the percentage of thick white in total white of eggs.

Knox and Godfrey (1938) confirmed their earlier observations (1933, 1934) to the effect that the percentage of thick white was not related to egg weight nor egg production. It was found, however, that the percentage of thick white in total white tended to decrease in the eggs of hens and pullets from the time that laying commenced up to July in the case of the hens and June in the case of the pullets. These observations indicate that a lowering of the percentage of thick white in total white is not due entirely to changes in temperature, as indicated by the observations of Lorenz and Almquist (1936), inasmuch as the temperatures during July and August where Knox and Godfrey worked are usually higher than the temperatures during June. Knox

nd Godfrey's data indicated quite definitely, however, that the per-ntage of thick white in total white is a heritable characteristic. nox and Godfrey (1940) have succeeded in developing two strains ffering significantly in the percentage of thick white in total white their eggs, one strain averaging approximately 45 per cent thick hite and the other strain approximating 65 per cent thick white, as own in Fig. 59.

Knox and Godfrey (1940) have stated that the selection of breed-g stock to develop these strains differing in percentage of thick hite consisted of selecting proved sires and dams, determined by rogeny testing, insofar as possible. In some instances the average ercentage of thick white in the eggs of the sisters of males and males was used as the basis of selecting future sires and dams. Occasionally a female was selected for breeding purposes upon the basis f the percentage of thick white of her own eggs. It is stated that a ertain amount of inbreeding was practiced.

ABNORMAL EGGS

In almost every flock abnormal eggs of one kind or another are ometimes produced. For the most part the laying of an abnormal gg is the result of some physiological disturbance, but since it is robably true that none of these abnormal egg characters is inherited hey are reviewed here only briefly.

Abnormal eggs are of four major kinds: (1) dwarf eggs; (2) eggs vith two or more yolks; (3) eggs within eggs; (4) abnormally shaped eggs.

Dwarf Eggs. Dwarf eggs probably occur more frequently than ll other kinds of abnormal eggs. Dwarf eggs have been studied by Pearl and Curtis (1916), who observed that 35.03 per cent of the dwarf eggs contained no yolks, 55.11 per cent contained a membrane-less fragment of yolk, and 9.85 per cent contained a small yolk enclosed in a vitelline membrane. Dwarf eggs differ in respect to size and shape and, frequently, also in internal structure. Only in a few cases did Pearl and Curtis (1916) find that dwarf eggs were produced by hens with abnormal laying organs. Apparently dwarf eggs result from the secretion of albumen, shell membranes, and shell as a result of a stimulus having been exerted upon the oviduct, though in many cases no yolk at all or only a small portion of yolk is present. Asmundson (1931*a*) states that the production of dwarf eggs gen-erally follows the ovulation of yolks that subsequently escape into the body cavity of the bird either intact or after the rupture of the vitelline membrane.

Féré (1898) claimed that the eggs at either end of the litter are smaller than the intermediate ones, but Warner and Kirkpatrick (1916) found that neither small nor large eggs are necessarily laid at the beginning or end of a hen's laying period but are more likely to be laid during the time of heavy production. Apparently the production of dwarf eggs is not an inherited tendency.

Eggs with Two or More Yolks. The laying of eggs with two yolks contained in one shell is of relatively common occurrence, some birds showing a greater tendency to produce double-yolked eggs than other birds. At the same time, no evidence has ever been submitted to show that this tendency is inherited. The most common cause of double-yolked eggs, according to Curtis (1915*a*), is the fact that a yolk liberated from the ovary one day may be arrested in its progress down the oviduct so that the yolk liberated from the ovary the next day overtakes the first one and both are enclosed in the same shell membrane and shell.

Conrad and Warren (1940) observed that over a two-year period about 65 per cent of all double-yolked eggs resulted from the simultaneous development of two ova. Approximately another 25 per cent of all double-yolked eggs resulted from the simultaneous ovulation of two yolks, one of which would normally have been ovulated the next day; there was thus a pause of one day before another egg was laid. Approximately 10 per cent of all double-yolked eggs resulted either from a one-day delay in the ovulation of one yolk so that two yolks were ovulated simultaneously, or from the fact that an ovulated yolk dropped into the body cavity and was taken up by the oviduct at the time of the ovulation of another yolk the next day.

Triple-yolked eggs have also been reported; they apparently owe their origin to the same causes that produce double-yolked eggs.

Eggs Within Eggs. Cases have been reported from time to time of a complete egg being surrounded by another egg. According to Curtis (1916), sometimes the enclosing egg is normal, although frequently a yolk is not present, and sometimes the enclosed egg is a dwarf egg or a normal one. Asmundson (1931*a*) has described these and other cases of double eggs quite fully, but since their production seems to be due almost entirely to abnormal functioning of the oviduct, without any indications of being inherited, they are not discussed further here. For other references, see Asmundson (1933). An interesting case of an unruptured follicle containing a yolk apparently fully formed laid by a Leghorn hen has been reported by Hutt (1939).

Abnormally Shaped Eggs. Occasionally in almost any flock an egg is laid flattened on one side or with a stalk attached or with some other deformity. Such eggs are either the result of a disturbance in the normal activity of the oviduct or are due to yolk or albumen material lying in proximity to a normal egg, thus causing a stimulus which leads to the formation of shell material around the extra yolk or albumen and thereby gives rise to a stalk attached to the egg.

PROBLEMS

1. Enumerate the more important factors that affect the weight of eggs laid by a given bird during her first laying year.

2. What is the relationship between egg production and egg weight during the first laying year?

3. Which part of the egg seems to be more readily controlled by breeding than other parts?

4. (*a*) Give at least two reasons why egg weight seems to be associated with body weight among birds of the same breed.

(*b*) Why is it that birds belonging to different breeds frequently differ significantly in body weight but lay eggs of approximately the same size?

5. What are the more important steps in breeding by which a poultry breeder may increase the average weight of the eggs laid by the birds of his flock?

6. What is the minimum number of eggs that must be weighed and what portion of the first-year production of a bird should they represent in order that the annual mean egg weight of a bird may be approximated?

7. What is the proper basis for determining the inheritance of egg weight?

8. Of what importance is it to know how egg shape is inherited?

9. How can a breeder of White Leghorns most efficiently develop a flock which will never produce any tinted-shelled eggs?

10. Has the production of abnormal eggs by a breeder's flock any particular significance in his breeding operations?

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CHAPTER IX

BREEDING PRACTICE

Except for the relatively few who can afford to indulge their interests in the breeding of poultry regardless of economic returns, the aim of practically every poultry breeder is to make the poultry-breeding operations as profitable as possible. Poultry breeding may be carried on with any of the following objectives in mind: the production of standardbred stock primarily for show purposes, the production of hatching eggs, the production of breeding stock, the production of laying pullets, the production of market eggs, and the production of poultry meat. Whatever may be the objective, the incentive is always the same, satisfactory financial returns on the money invested in the breeding operations. Also, whatever may be the objective, the fundamental principles of breeding that determine the results secured remain the same.

In order to achieve progress, it is necessary for the poultry breeder to be able to identify superior-breeding males and females and to mate them in such a way that they will produce the largest possible number of progeny possessing the desirable characters for which the stock is being bred. The ability to identify males and females of superior breeding worth is the first requisite of a successful breeding program. This is just as true in breeding for perfection in standardbred excellence as in breeding for excellence in egg production. In many flocks, far too many birds of inferior breeding worth are used each year because many poultry breeders apparently have never adopted a logical basis on which to select their breeding stock. Mediocrity tends to reproduce itself. The results secured from many matings are largely matters of chance because in too many cases, the matings are made by guesswork, due to an insecure amount of evidence upon which to base the intelligent selection of the proper kind of males and females to mate together. How to eliminate some of the guesswork in selecting breeding stock and how to mate males and females of superior breeding worth for the development of superior strains is related in the following pages.

The Practical Significance of Variation. The fact that there is great variation among fowls is of particular significance in inheritance. Without variation, progress in breeding work would be impos-

sible. Without variation, the selection of superior individuals would be impossible. Without selection, improvement is impossible. Variation makes selection possible and selection makes improvement possible.

As Lush (1937) has said: "Variation is the raw material on which the breeder works." In almost any flock of birds, there is nearly always sufficient variation so that the least desirable individuals can be segregated from the most desirable ones. But the poultry breeder must always keep in mind that, except for most of the color characters and certain of the morphological characters, the actual differences between two individuals are caused partly by environmental influences as well as by heredity. It has been observed in previous chapters that environmental influences exercise their effects on such characters as hatchability, rate of growth, egg production and egg weight. This makes the problem of selecting birds for breeding purposes more difficult because the poultry breeder may mistake the effects of the environment for the effects of the genes and thus save some birds that will prove to be poor breeders.

The Possibilities of Selection. As far as the various physiological characters are concerned, it is safe to say that any two birds will differ genetically to a greater or lesser degree. The problem of the poultry breeder is to be able to identify which of the two is superior in its ability to transmit the desirable genes. It should be kept in mind, however, that selection can do nothing toward creating new genes. Nevertheless, the selection of the best individuals for future breeding purposes makes possible the segregation of desirable genes from each of the parents and the recombination of these desirable genes in the progeny.

One of the inherent difficulties involved in poultry-breeding practice is that the poultry breeder usually considers several different characters simultaneously when he is making his selections. What he should keep in mind is that the larger the number of characters on which selection is based, the lower the intensity of selection for each of the characters that he is endeavoring to improve by selection. In other words, the more attention paid to unimportant characters, the less valuable is the selection for the economically more important characters.

Since the average poultry breeder is desirous of maintaining excellence with respect to each of several characters, such as high hatchability of eggs, good viability in chicks, low mortality in pullets, good egg production, and good egg size, it is obvious that a very large number of genes is involved, inasmuch as there is probably a large number of genes responsible for the development of each of these

characters. Very rarely indeed does any individual bird excel in all or even most of the characters; in fact, most birds excel in but few characters. It follows, therefore, that the genes that determine these characters are in varying degrees of heterozygosity in practically all birds. The object of the poultry breeder is to produce birds each having as many as possible of the desirable genes. In other words, homozygosity of desirable genes in each bird is the desired goal.

There are several obstacles, however, that prevent the average poultry breeder from being able to select from among all the birds he has those which when used as breeders would produce the kind of progeny posessing to a high degree the various economic qualities desired. The difficulty of deciding upon how much importance should be attached to minor points of breed and variety characteristics, such as the number of serrations on the comb, side-sprigs, stubs, and plumage coloration, often leads to the sacrifice of birds of real value from the standpoint of transmitting qualities of economic importance. Selecting birds on the basis of their relative perfection in breed and variety characteristics is commendable enough in itself, but the object lesson for the poultry breeder is that the more attention given to these matters the less progress can be expected in breeding for purely economic qualities.

Another obstacle in selecting the potentially best breeders in the flock is that the record of production or the performance of the individual often serves as a very poor criterion of breeding worth. In Chapter VII, this has been shown to be true with respect to individual records of egg production, when the females used as breeders were selected on the basis of having laid a minimum of 200 eggs each during their first laying year, as is the case with most poultry breeders who endeavor to develop a high laying strain. Available evidence also suggests that individual records of hatchability, egg size, and other physiological characteristics often do not serve as an indication of breeding worth.

The pedigree of an individual often gives a false sense of security regarding its breeding worth. Usually the pedigree contains little information about the qualities of the collateral relatives of the various ancestors and practically no information regarding the breeding worth of the ancestors.

The most reliable criterion in evaluating the breeding worth of males and females that have been used as breeders is the progeny test. There is nothing mysterious about progeny testing for the selection of future breeders. The principle involved can be illustrated by reference to practical experience. The Wyandottes have rose combs, but occa-

ionally birds with single combs appear among the progeny secured rom a mating of a Wyandotte male and female. Since rose comb is lominant to single comb, there being but a single gene difference, it is bvious that the male and female parents were each heterozygous for ose comb. They each had a gene for rose comb and for single comb ut had rose combs because the gene for rose comb is dominant to the ene for single comb.

It is most important to bear in mind the fact that these Wyandottes eterozygous for rose comb could not be distinguished in appearance rom Wyandottes homozygous for rose comb. The only way they ould be distinguished is by a breeding test. The birds heterozygous or rose comb, when mated together, would produce progeny in the roportion of three with rose combs to one with single combs. Birds omozygous for rose comb when mated to single-comb birds would produce only rose-comb progeny, but birds heterozygous for rose comb, when mated to single-comb birds, would produce approximately equal numbers of rose-comb and single-comb birds. The progeny test indicates the genetic constitution of the parental stock as far as comb type is concerned.

So it is with respect to practically all other characters which it is desired to develop in a strain. Neither the performance record nor the pedigree serves as a reliable criterion of the breeding worth of an individual, although both provide useful information when considered in relation to the results secured from progeny testing. Lush (1935) has pointed out that the progeny test is needed most for characters which can only be expressed in one sex, such as egg production, and for characters which are only slightly hereditary. Records dealing with such characters as body size, egg size, and egg production are necessary, of course, in making the original selection of birds to be discarded and of those to be kept for breeding purposes. Pedigrees are necessary if the poultry breeder wishes to practice inbreeding or avoid too close inbreeding.

Inbreeding and Its Effects. Inasmuch as inbreeding is the mating together of related individuals, it is obvious that the closer the degree of inbreeding the greater the number of genes in a homozygous condition in the progeny for the simple reason that the more closely related the parents are the greater is the number of similar genes that are brought together in the matings. The closest form of inbreeding is the mating of a full-brother to a full-sister, and the next closest form is the mating of a sire to his daughter or a dam to her son. The pedigree of a bird secured from any of these closely inbred matings shows the same ancestor appearing in the pedigree more than

once, so that there are fewer different ancestors than in the pedigree of a bird whose parents were unrelated.

$$G\begin{cases}E\,♂ & \begin{cases}C\,♂ & \begin{cases}A\,♂\\B\,♀\end{cases}\\D\,♀ & \begin{cases}A\,♂\\B\,♀\end{cases}\end{cases}\\ F\,♀ & \begin{cases}C\,♂ & \begin{cases}A\,♂\\B\,♀\end{cases}\\D\,♀ & \begin{cases}A\,♂\\B\,♀\end{cases}\end{cases}\end{cases}\qquad V\begin{cases}T\,♂ & \begin{cases}P\,♂ & \begin{cases}H\,♂\\I\,♀\end{cases}\\Q\,♀ & \begin{cases}J\,♂\\K\,♀\end{cases}\end{cases}\\ U\,♀ & \begin{cases}R\,♂ & \begin{cases}L\,♂\\M\,♀\end{cases}\\S\,♀ & \begin{cases}N\,♂\\O\,♀\end{cases}\end{cases}\end{cases}$$

In the above diagrams, bird G is shown to be the product of a mating of a full-brother to a full-sister for two generations; his great grandsire and great grandam each appear four times in the pedigree, and his grandsire and grandam each appear twice. Individuals having common ancestors tend to have more genes in a homozygous condition than individuals that do not have common ancestors. Bird V has no common ancestors in his pedigree.

From the practical standpoint, the results secured in experiments on inbreeding are of interest to the poultry breeder because he frequently is in a quandary as to whether he should use breeding stock within his own flock or purchase breeding stock from an outside source. He is also frequently in a quandary as to whether or not he should mate males and females that are related. If such be desirable for the particular purpose in mind, there is still the question as to how closely related the males and females may be in order to secure the most satisfactory results. Should a sire be mated to his daughters, dam to son, brother to sister, or cousin to cousin, in an effort to improve egg production in a flock of birds? These are some of the questions in the minds of poultry breeders with the approach of every breeding season.

It should be borne in mind that inbreeding brings together undesirable as well as desirable genes. Since many recessive genes have less desirable effects than dominant genes, inbreeding has the effect of unmasking the presence of these undesirable recessive genes whose effects were masked by the presence of desirable dominant genes. It is when these undesirable recessive genes occur in a homozygous condition that they are able to produce undesirable characters, as has been shown in the preceding pages, especially with such characters as hatchability of eggs and viability of chicks. It should be borne in mind, however, that the results secured from experiments on inbreeding have been secured for the most part from the closest forms of inbreeding. The poultry breeder who has a relatively large number of breed-

ing birds to use each year could safely practice inbreeding to some extent, but he should practice rigid selection of his young and old stock for future breeding purposes.

If undesirable characters appear in inbred birds, it is because undesirable genes existed in the original stock. The appearance of undesirable characters in inbred strains makes it possible for the poultry breeder to eliminate rather quickly numerous undesirable characters from his flock. Inbreeding, if accompanied by intelligent selection, makes rapid improvement possible because superior families can be readily separated from inferior families.

The Advantages of Linebreeding. Among the various ways in which inbreeding can be carried on is to use one individual repeatedly in the breeding project. Cattle breeders have been known to use a certain bull for several generations, and horse breeders have sometimes done the same thing with an outstanding stallion. The practice of breeding back to a given ancestor has been called linebreeding; in reality it is simply a special method of inbreeding.

A practical method of linebreeding has been presented by Knox (1929). Instead of following the usual method of mating a number of cockerels of average quality to his entire flock of females, one male, called the foundation male, of outstanding value is purchased from a reliable breeder and is mated to some fifteen of the best hens selected from the entire flock. This mating is best made in a colony house separate from the large flock. The cockerels secured from this mating are selected carefully and are saved for mating the next year to a selected group of hens in the large flock. The pullets secured from the colony-house mating are put into the large poultry house with the hens selected from the previous year and with the pullets secured from the large flock mating.

During the second year of the linebreeding project, the foundation male is again mated in the colony house to the best hens kept over from the previous year; these may include a few two-year-old hens from the original colony-house mating and the best yearling hens from the large flock. The selected cockerels and pullets produced by the second-year colony-house mating are put with the larger flock in the fall of the year. The selected cockerels secured from the colony-house mating of the previous year are mated to a selected group of hens in the large flock, which the farmer can keep separated from the rest of the flock during the breeding season. In this way some of the heritable characters of the foundation male become intensified in the progeny of the whole flock. The reason for mating the selected cockerels secured from the colony-house mating the previous year to selected hens only

in the large flock is that selected hens should produce better chick than unselected hens and pullets, and, moreover, the large flock ma contain a number of full-sisters and half-sisters of the cockerels. Th mating of the cockerels to selected hens avoids the danger of harmfu effects resulting from brother × sister matings.

During the third year the same methods are followed, and, sinc the colony-house mating consists mostly of the very best hens selecte

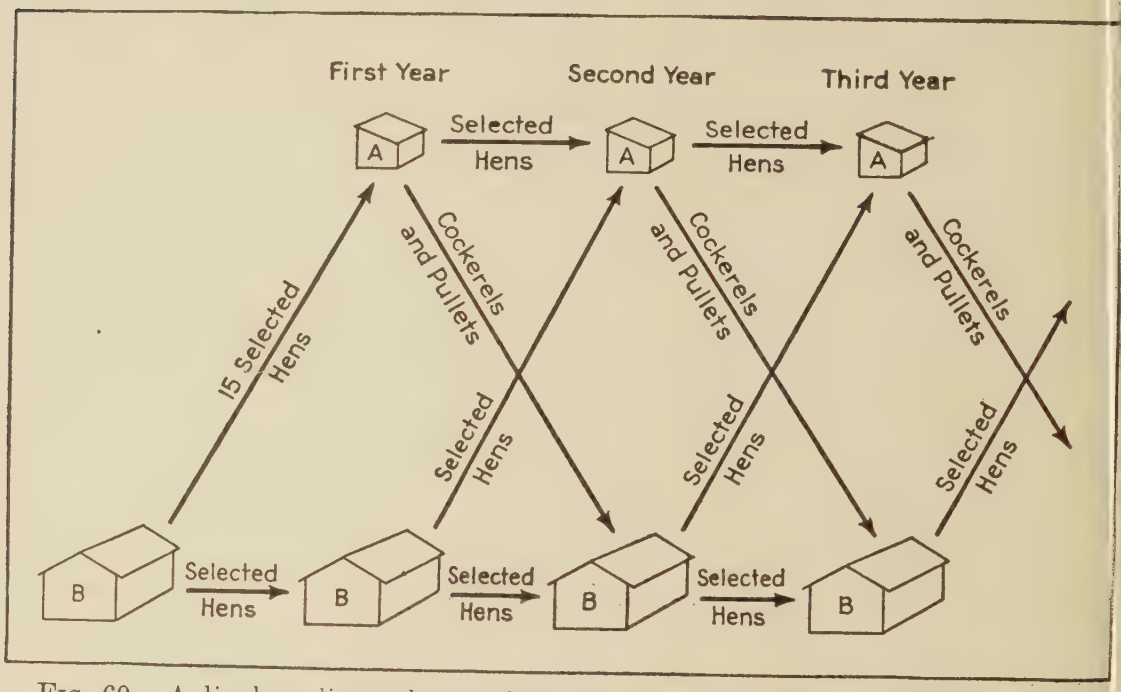


Fig. 60. A linebreeding scheme that provides for the mating each year of a few of the very best females of the entire flock to a foundation male in a colony-house designated A. Each year the pullets and a few selected cockerels produced by the colony-house mating are placed with the rest of the flock in the laying house designated B. During each breeding season, after the very best females have been selected for the colony-house mating, a second best group should be selected and kept separate from the other hens and from the pullets and should be mated to cockerels secured from the colony-house mating. (Knox, 1929.)

from the large flock, some of these hens should be daughters of the foundation male, provided, of course, that he actually proved to be a good breeder; these daughters would have been produced in the first year of the colony-house mating. During the third year the foundation male would in all probability be mated to a number of his granddaughters, females produced by the mating of the sons of the foundation male to selected hens in the large flock during the second year.

If the foundation male was used in the colony-house mating during the fourth and later years, he would in all probability be mated to related descendants only, unless a few three- or four-year-old hens from the original flock were still on hand.

This linebreeding program has the advantage of requiring the

farmer to buy only one good male, for which he should be willing to pay a good price, instead of purchasing several medium-priced males of mediocre value, and the program also has the distinct advantage of obliging the farmer to select his best hens for the purpose of mating them to the foundation male. Another advantage is that the best females of the entire flock are bred back to the foundation male, thus making possible the distribution of the desirable heritable characters possessed by the foundation male to every member of the flock.

Such a definite linebreeding project can be carried on as long as the foundation male lives and is able to produce a high proportion of fertile eggs, provided, of course, that he proves to be a valuable breeder as determined by the egg production of his pullets. Should the foundation male prove to be a poor breeder, another one should be secured for the next year.

This plan of linebreeding could be carried on by the commercial poultry breeder, who, however, would probably want to make several colony-house matings each year.

Crossbreeding and Its Effects. Crossbreeding is the mating of birds belonging to different breeds, so that the natural result is to combine many different genes from rather widely separated sources. Since the characters in each of the purebred parents are due, for the most part, to the effects of dominant genes, it is obvious that the progeny of a crossbred mating contains many dominant genes in a heterozygous condition, some of the dominant genes having been received from one purebred parent and some from the other. Many dominant genes produce more favorable effects than do recessive genes, so that progeny produced by crossbreeding is usually superior in many characters over either of the parental breeds crossed. This superiority is said to be due to heterosis or hybrid vigor, the term "hybrid" designating the progeny of a crossbred mating.

The real purpose of crossbreeding is to provide for the combination of desirable qualities from two distinct lines of stock. At the same time, very little is to be gained by crossing animals that have not been carefully selected. Jones (1925) points out that "Uniform progeny are produced only when the parental races are fixed in their particular type and breed true, and it is only when they are from separate and different lines of descent that decidedly beneficial results from crossing can be expected."

Naturally, crossbreeding tends to lower the breeding value of the hybrid progeny by making the progeny more heterozygous and by making selection among the progeny less effective. Inasmuch as the hybrid progeny resulting from crossbreeding should not be used for

breeding purposes, it is obvious that a purebred flock must be maintained of each of the parental breeds used to make the cross. This means that the poultry breeder would have to maintain two purebred flocks and provide room for the hybrid progeny. Maintaining two separate breeding flocks constitutes a distinct handicap for the individual breeder in his breeding operations because fewer progeny could be raised from each purebred flock and because there would be less chance for selection than if only one purebred flock was maintained and crossbreeding was not practiced. However, farmers, broiler raisers and commercial poultrymen who do not breed their own flocks but rely upon the breeder or commercial hatchery as a source of baby chicks each year often find the purchase of crossbred chicks advantageous.

METHOD OF MATING TO PRACTICE

Whatever may be the methods used in selecting the breeding stock or the system of breeding employed, it is obvious that proper methods of mating must be employed or the results in the reproduction of the flock from year to year will not be satisfactory.

Not only should the breeding stock used each year give good results in respect to the fertility and hatchability of the eggs set and the viability of the chicks hatched, but also improvement should result in the quality of the stock produced each year. If progress is not achieved from year to year, then something is inherently wrong with the stock being bred from; or the selection of the breeding stock each year is not founded upon sound principles; or the system of breeding is at fault; or improper methods of mating are used; or any combination of these circumstances may prevail. It is most necessary, therefore, that the progressive breeder know the kind of stock he is dealing with and that he use intelligent methods of mating.

Mass Matings for Numerous Progeny. The term "mass mating" simply means that a number of males are allowed to run with the entire flock of females. Such matings are usually made for the purpose of securing the largest possible number of fertile eggs. No pedigree breeding work can be carried on because the male parentage of the chicks is unknown, and if the females are not trap-nested, the female parentage of the chicks also is unknown. Mass matings are practiced for the most part by commercial and farm poultry raisers. When all other conditions are satisfactory, the percentage of fertile eggs is usually higher in mass matings than in any other method of mating.

The number of males to use in a flock depends on the size of the flock and the breed. The approximate proportion should be about as

follows: Brahmas and similar breeds, 1 male to 8 to 12 females; Plymouth Rocks and similar breeds, 1 male to 10 to 15 females; Leghorns and similar breeds, 1 male to 12 to 20 females. Best results in fertility can be obtained by keeping two sets of males, using each set on alternate days or in alternate periods of three or four days.

Where several males are mated to a large flock of females, it is well to place temporary board partitions about 8 to 12 feet long and 2 feet high in different parts of the house and yard in order to avoid too much interference in mating.

Although mass matings are required for the production of numerous progeny, the fact is obvious that if the poultryman would divide his flock into two parts and breed only from the best birds he would make much more progress than by mating all the females in the flock. The use of the entire flock means that many birds of mediocre quality are mated, with the result that their progeny tends to lower the average quality of all progeny produced. In order to get the best results possible in mass matings, both males and females should be selected carefully; especially is this important in the case of the males.

Pen Mating for Quality Progeny. By the term "pen mating" is meant the system of mating a pen of females to a single male. Those who practice pen mating usually undertake pedigree breeding work, in which case it is necessary to know the ancestry of every chick hatched. The number of females in the pen may vary from about 8 to 20, depending upon the breed. It occasionally happens that a certain female may not mate freely with a certain male but will mate with another male quite readily. Preferential matings have been observed by Philips (1919), Upp (1928), and Warren and Kilpatrick (1929); difficulties encountered in this respect can be overcome by moving the female from one pen to another.

Occasionally poultry breeders make up pen matings consisting of about 20 to 25 females and males that are full-brothers. The pedigree of the chick can be given for all the ancestry except the male, and this feature often makes the practice of doubtful value because full-brothers frequently give very different results when bred to the same females.

Since a pen mating is made up for the express purpose of producing progeny of superior quality, the most careful selection of the females and the male should be made. Since all the progeny of a pen receive one-half of their heritable characters from the sire, his selection is of paramount importance.

Stud Mating and Its Value. The term "stud mating" is used in those cases where females are mated individually with a male kept by himself in a coop or a pen. This method can be used only where the

females are trap-nested, each female being mated to a male when she is taken from the trap nest. One advantage in stud mating is that the females to be mated to each male do not have to be kept in separate pens, such an arrangement making it unnecessary to build a colony house or provide a separate pen for each breeding flock. Another advantage of stud mating is that more females can be mated with one male than in pen mating.

The time of mating can be distributed evenly throughout the day thus enhancing the male's reproductive ability. Philips (1918) observed that a White Leghorn male mated as many as 38 times a day with White Leghorn females. Martin and Anderson (1918) report that of 34 White Leghorn females mated by a single male in one day only 10 laid fertile eggs, thus showing the inadvisability of too frequent matings on the part of the male. Craft, McElroy, and Penquite (1926) show that males which are excessively active produce a larger percentage of dead and weak spermatozoa than males which mate less frequently. Fronda (1926) has observed that one mating each week is sufficient to produce good fertility but two matings each week would undoubtedly be better. It is easily seen that stud mating, when properly employed, tends to conserve the reproductive ability of the male.

One important thing to be kept in mind when stud mating is practiced is that the males must be kept in good physical condition. Keeping a male confined in a small coop during the entire breeding season is apt to lead to the production of a high percentage of infertile eggs toward the latter part of the season.

Although it is true that stud mating avoids the necessity of separating the females into small flocks there is the important factor to be considered that considerable time and labor are required to mate each female individually with a male.

Practicing Artificial Insemination. Female breeders are sometimes artificially inseminated with semen from males that are either so much smaller or so much larger than females to which they are mated that natural mating is impossible. Females kept in laying cages are sometimes artificially inseminated. The practice of artificial insemination is also resorted to by investigators when crossing widely separated groups such as the chicken and guinea-fowl, the chicken and pheasant, and the chicken and the peafowl. Hagedoorn (1939) has pointed out that mixed semen from several males injected into a group of females will give results more nearly in keeping with the genotype of these females than when they are mated to a single male.

The early artificial insemination experiments of Ivanov (1913)

were followed by those of Payne (1914), Amantea (1932), Craft, McElroy, and Penquite (1926), Dunn (1927), Ishsikawa (1930), Jull and Quinn (1931), Nikitina (1932), Bernshtein (1933), Adamstone and Card (1934), Warren and Scott (1935), Grodzinski and Marchlewski (1935), Burrows and Quinn (1935, 1937, 1938, 1939), and Bonadonna (1939). Various methods of obtaining semen from males and different methods of administering the semen to females have been employed by the investigators mentioned, but the extensive investigations of Burrows and Quinn have resulted in the development of a technique that gives very satisfactory results. Parker (1939) has described an apparatus for the collection of semen.

Lack of space makes it impossible to give the detailed instructions for holding the birds and for collecting and injecting semen, but these instructions can be obtained in bulletin form from the United States Department of Agriculture. A few general observations, taken from Burrows and Quinn (1939) with slight changes, are given here. Experience in handling the males used as a source of semen and the females to be inseminated is necessary in order to secure good fertility in the eggs laid by the inseminated females. Semen contaminated with urine and feces should be avoided. The semen is collected in a glass tube and should be placed in the oviduct by using a syringe, sufficient pressure being applied so that the oviduct will protrude enough to allow about one inch of the syringe to enter the orifice of the oviduct. The semen should be forced from the syringe while the oviduct is still protruded. Good fertility is usually obtained by the injection once a week of a dose of 0.1 cubic centimeter of semen. In some cases, however, more frequent inseminations of larger doses have been found necessary.

Grodzinski and Marchlewski (1935) found that the sperm could be diluted from 10 to 20 times with the following diluting solutions, ranked according to their relative ability to maintain sperm motility, blood serum, embryonic extract, and albumen. Sperm diluted with egg albumen preserved its motility the longest when the material was kept at a temperature of 60.8° F. Sperm diluted with blood serum and embryonic extract preserved its motility the longest when the material was kept at 98.6° F. The duration of the fertilizing capacity of the diluted sperm was not tested.

Bonnier and Trulsson (1939) diluted the semen in Ringer solution in sperm concentrations of 30, 10, and 2 per cent and found that a solution containing 30 per cent semen gave better results than undiluted semen and that a solution of 10 per cent semen gave as good results as undiluted semen. The highest fertility was obtained when

two days were allowed to elapse between the day of egg laying and the day of insemination.

SECURING GOOD FERTILITY

In order that best results may be secured from any method of mating that may be employed, the poultry breeder should always keep in mind a number of factors that affect the number of progeny secured. The proper management of the breeding stock is of great importance in securing the largest possible number of good chicks in proportion to the eggs set. The proper care of the male breeder is especially important, since he is the sire of every chick from each of the females in a pen. The male should get plenty to eat at all times during the breeding season. It is sometimes desirable to cut off the spurs of old males otherwise the females are apt to be torn. In northern parts of the country the males are apt to have their combs and wattles badly frozen, to such an extent sometimes that they will not mate with the females. Payne and Ingram (1927) have shown, however, that a moderate amount of freezing of the comb reduced fertility and hatchability below normal for only eleven days. To avoid the danger of having combs badly frozen, some poultry breeders cut off the combs of males in the fall of the year, this practice being called "dubbing." It is also practiced occasionally on old males, whose reproductive ability has apparently become reduced.

Hays and Sanborn (1939) found that, when the average temperature during the period that hatching eggs were laid was below 32° F., the average fertility ranged between 54 and 77 per cent, whereas when the average temperature rose to above freezing the fertility ranged from 70 to 85 per cent.

Unless the conditions under which the breeders are kept are almost ideal, fertility may be adversely affected. The breeders must be healthy and vigorous and must be kept in clean, well-ventilated houses. The houses should be kept free of mites and the birds free of lice. If the litter in the breeding house is allowed to become filthy, the fertility of the eggs may be lowered.

Physiological Aspects of Fertility. That males and females both differ among themselves regarding their ability to produce fertile eggs is well known, but as to the causes of these differences very little is known. Craft, McElroy, and Penquite (1926) found no definite evidence that the kind of ration fed to male birds has any effect on the number or fertilizing ability of the spermatozoa. Hutt (1929) found that partially castrated cocks and normal cocks produced practically the same results in fertility. Hutt also found that fertility in

the male fowl is not dependent upon the size of the testes, and he points out that data submitted by Craft, McElroy, and Penquite bear out the same point. The relative number of spermatozoa per given unit of semen was found not to bear any relation to fertility, this observation also being borne out by the results secured by Penquite, Craft, and Thompson (1930). Hutt suggests that in the male fowl fertility is dependent upon the physiological efficiency of the spermatozoa rather than upon their quantitative production.

Dunn (1927) observed evidences of selective fertilization taking place when Single-Comb White Leghorn females were first mated to a full-brother and then to a Rose-Comb Hamburg male. One group of females thus mated produced chicks over 97 per cent of which were sired by the Single-Comb White Leghorn full-brother, whereas in another group of females two-thirds of the chicks were sired by the Rose-Comb Hamburg male.

Jull (1930) found that when strains of birds that had been closely inbred for three generations were intercrossed the fertility of the eggs was significantly lower than in the inbred matings of the previous year.

According to the observations of Jull (1935*a*) and Hays and Sanborn (1939), fertility tends to decline with the increase in the age of the breeders.

Burrows and Titus (1939) observed that crossbred cockerels at 275 days of age produced, on the average, 1.0 cubic centimeter of semen at each collecting time.

TABLE 54. PERCENTAGE OF FERTILITY OF DAMS ACCORDING TO AGE, MATED TO COCKERELS

(Jull, 1935*a*)

Breed	No.	Age	Fertility	No.	Age	Fertility
White Leghorn	60	Pullets	95.4	129	Yearlings	89.3
		Yearlings	91.8		Two-years	88.2
Rhode Island Red	7	Pullets	93.0	71	Yearlings	93.0
		Yearlings	90.0		Two-years	88.2
Barred Plymouth Rock	35	Pullets	79.7	12	Yearlings	84.9
		Yearlings	82.2		Two-years	86.7

Hays and Sanborn (1939) observed that in most cases of sterile matings the male was responsible, for, when a female producing infer-

tile eggs was shifted to another male, fertile eggs were produced in nearly every case.

Fertility is not inherited, according to Pearl and Surface (1909), Hays and Sanborn (1924, 1939) and Jull (1935). The poultry breeder who wants to make sure that maximum fertility will result from a given mating should make up the mating several weeks before the regular breeding season and test the eggs for fertility. This provides sufficient time before the regular breeding season to make any necessary changes.

Good Fertility in Five Days. It is well for the poultry breeder to know how soon fertility may be expected after the males have been placed with the females. That a fertile egg may be produced shortly after copulation takes place has been demonstrated by the following investigators, the number of hours elapsing from the time of copulation to the laying of the first fertile egg being given after the investigator's name: Gilbert (1905), 39 to 65; Pearl and Surface (1909), 72; Coste and Gerk (1910), 28; Philips (1918), 23; Erickson (1924), 72; Fronda (1926), 20; and Dunn (1927), 21. It should be noted that the observations of Coste and Gerk, Philips, Fronda, and Dunn were based on individual matings, whereas all other observations were based on pen matings. Curtis and Lambert (1929) observed that the onset of fertile production ranged from 24 hours to 7 days, with 57.1 hours as the average.

Waite (1911) from a flock of 20 White Leghorn pullets secured 50 per cent fertile eggs on the third day and 70 per cent fertile eggs on the fourth day after mating. Crew (1926) reports that maximum fertility is reached by the end of the first week after mating. From the practical standpoint, therefore, it may be stated that eggs may be saved for incubation beginning about the fifth day after the males have been placed with the females. More time should be allowed when cock birds are used.

Good Fertility Two Weeks After Matings Discontinued. The length of time that fertile eggs are produced after the pen mating has been discontinued is a matter of some practical importance, although usually the males are allowed to remain with the females as long as eggs are saved for incubation. Spallanzani (1784) reported that a hen can lay fertile eggs 20 days after being mated, and Crew (1926) secured a fertile egg 32 days after removal of the male, these observations being based on individual matings.

The number of days that fertility of eggs remained sufficiently high in order to be saved for incubation after the males were removed from the breeding pens has been reported as follows: Gilbert (1904, 1905),

11; Waite (1911), 11; Chapellier (1914), 10 to 18; Elford (1926), 19; Philips (1918), 15; Dunn (1927), 14. Lillie (1919) observed that after the end of the third week the vitality of the spermatozoa is considerably reduced. Curtis and Lambert (1929) observed that the mean duration of fertility was about 11 days, with 21 days as the extreme duration. It would seem, therefore, that reasonably good fertility may be expected for about two weeks after the discontinuance of the breeding pen.

When it is desired to substitute one male for another in the breeding pen and still have definite knowledge of the ancestry of the chicks hatched from both males, fertile eggs secured after the third week after the removal of the first male may be regarded as having been fertilized exclusively by the second male.

Carefully controlled tests have shown that if a male in a pen dies or is removed from the pen, and another male is placed in the pen immediately, the eggs laid by hens mated by both the first and second male are more likely to be fertilized by the spermatozoa of the second male, especially after a few days. Crew (1926) has observed that the influence of the first male is removed by the 7th to the 10th day, the exact time differing in different cases.

Warren and Kilpatrick (1929) mated a Single-Comb White Leghorn male and a Black Minorca male alternately with Black Minorca and Jersey Black Giant females and observed that the spermatozoa of the male making the second mating soon replaced the spermatozoa of the male making the first mating in fertilizing the eggs, and that there was practically no overlapping of the offspring produced by the two males.

Olsen and Knox (1938) demonstrated that eggs could be tested for fertility at from 16 to 20 hours of incubation at 100°F. An ordinary commercial candling lamp equipped with a 75-watt daylight bulb was all that was necessary, but it was found advantageous if a pair of dark blue glasses were also used.

BREEDING FOR HATCHABILITY

In the reproduction of the flock the object of the poultry breeder is to secure the greatest possible number of good chicks in proportion to the total number of eggs sets. Granted that everything possible has been done to secure good fertility in the eggs produced during the breeding season, the next step is to secure the best possible hatching results. Among the various factors affecting hatching results the most important is the hatchability of the eggs, other factors being conditions of incubation.

The term "hatchability" means the hatching qualities of an egg,

the greatest possible number of chicks that could be hatched from a given number of fertile eggs being desired. It is obvious, of course, that conditions of incubation, such as temperature, humidity, and ventilation, affect hatching results, but the discussion in this book is primarily concerned with those factors which determine whether or not a chick can hatch from a fertile egg incubated presumably under ideal conditions of incubation.

Egg Size and Hatchability. Although Benjamin (1920) found that egg size did not influence hatchability, the results secured by Dunn (1922) and others indicate that very small and very large eggs usually do not hatch as well as eggs between these extremes. Dunn's results also indicate that the deviations from the mean egg weight of the individual, rather than the deviation from the flock mean, influence hatchability. For each dam those of her eggs that were above her mean egg weight hatched less well than those of her eggs which were below her mean egg weight. Halbersleben and Mussehl (1921–22), Funk (1934), and Warren (1934) also observed that very large eggs failed to hatch as well as medium-sized eggs.

On the other hand, Jull and Haynes (1925) and Hays and Sumbardo (1927) secured results which indicated that among eggs fairly uniform in size, egg weight apparently did not influence hatchability materially. This was confirmed by Axelsson (1932) and Godfrey (1936), both of whom found that eggs approximating standard weight of 56.7 grams (2 ounces) per egg usually hatched the best.

Funk (1934) made extensive observations on the hatchability of the eggs of different breeds, the eggs being divided into the following four size groups: 54 grams or less, 55–58 grams, 59–61 grams, 62 grams or more. Hatchability was 78.1, 79.9, 75.8, and 68.1 per cent, respectively. Godfrey (1936) observed that among eggs averaging about 46 grams, the hatchability was approximately 51 per cent, among eggs weighing from about 52 to 58 grams the hatchability was approximately 75 per cent, and among eggs weighing over 58 grams, the hatchability decreased perceptibly. Hutt (1938) found that eggs weighing more than 60 grams had a significantly higher incidence of embryo head-under-left-wing malposition than smaller sized eggs.

The size of eggs used for incubation is very important because the results secured by Jull and Quinn (1925) and Upp (1928) and others show that there is a high correlation between the size of the chick and the size of the egg from which it is hatched. Moreover, since egg size is inherited, it is of considerable economic importance to use for incubation eggs weighing at least 2 ounces each and eggs from yearlings and

older hens that are used for incubation should preferably weigh 2.2 ounces each.

The progress achieved in breeding for increased egg size is shown graphically in Fig. 75. In this strain of White Leghorns, no efforts were made to increase egg size until the sixth generation, but thereafter the breeding stock used each year was selected on the family method devised by Goodale (1938). The family method of selecting breeding stock is essentially the progeny-test method and is explained in greater detail in the section of this chapter dealing with the subject of breeding for egg production.

Egg Shape and Hatchability. As far as the shape of eggs in relation to hatchability is concerned, Benjamin (1920), Jull and Haynes (1925), and Hays and Sumbardo (1927) came to the conclusion that egg shape had no influence on hatchability, at least as far as eggs showing a normal range of variability in shape is concerned. On the other hand, Landauer (1937) has pointed out that very long and narrow eggs seldom hatch.

Shell Characters and Hatchability. Dunn (1922) secured evidence indicating that eggs with highly porous shells do not hatch as well as eggs with normal shells. Hays and Sumbardo (1927) failed to disclose any relationship between thickness or porosity of shell and hatchability and Funk (1934) found no significant difference in the hatchability of eggs with poor shell texture and those with good shell texture, the texture of the shell being observed by candling.

Axelsson (1932) made observations on shell porosity in relation to hatchability, porosity being determined by the loss in weight in eggs held for 24 hours in a temperature averaging 71.6°F. and at a relative humidity of 60 per cent, and concluded that hens laying eggs with the least shell porosity had a better hatchability of their eggs than hens laying eggs with the greatest shell porosity. That high shell porosity tends to reduce hatchability was reported by Voitellier (1936) and Shibata and Murala (1936). Porosity of shell is inherited, but it is readily influenced by environment. The poultry breeder would do well to test a sufficient number of eggs from each hen for the purpose of determining whether or not any of them lay eggs having excessively high shell porosity.

Specific Gravity and Hatchability. In studies on the relationship between the specific gravity of eggs and their hatchability, Mussehl and Halbersleben (1923) observed that the specific gravity of the shell was twice that of the egg contents and that there was a low significant correlation between the specific gravity of the whole egg and hatchability. Munro (1939) has shown that the eggs of his

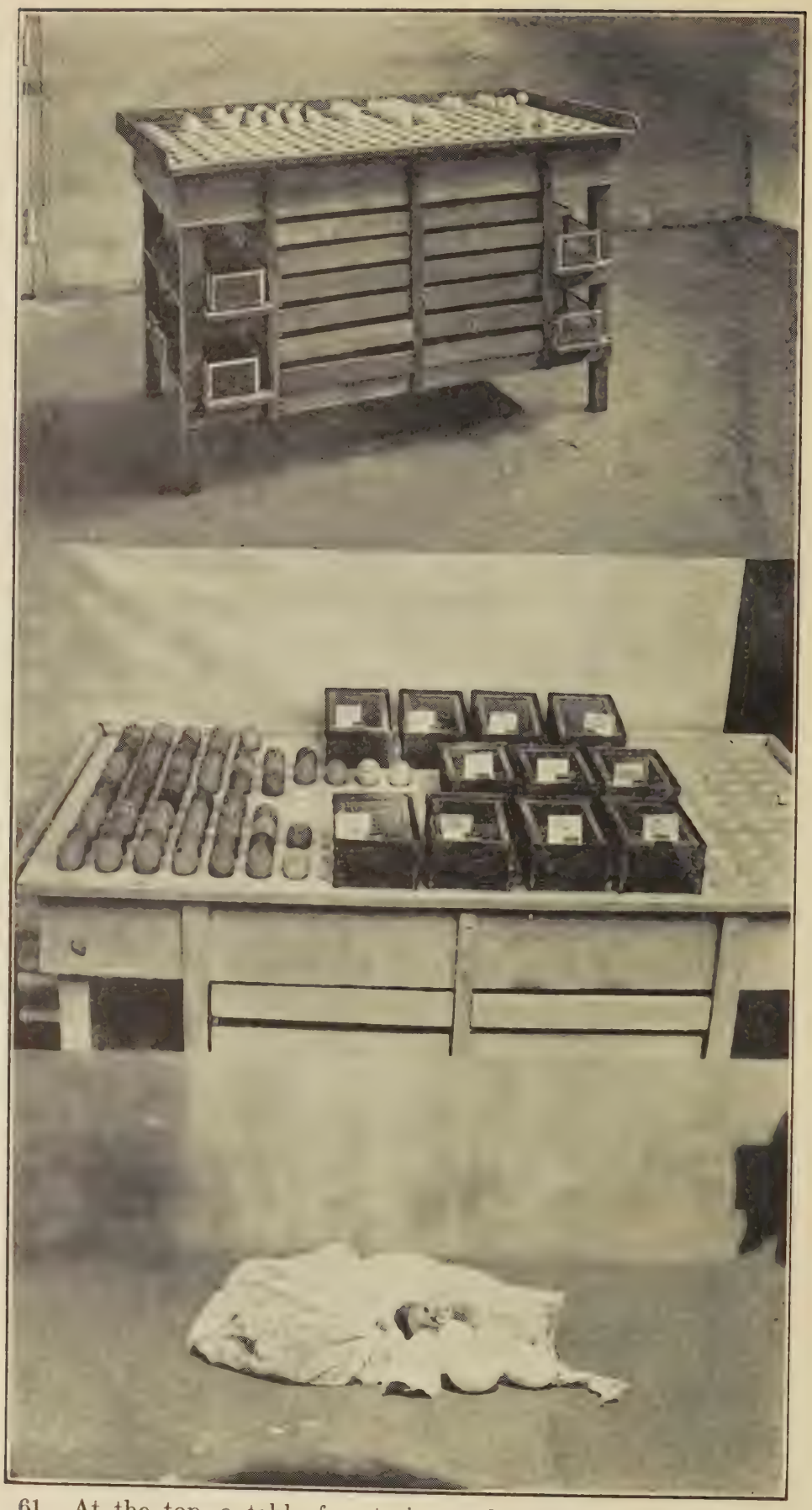


FIG. 61. At the top, a table for storing and sorting hatching eggs. In the center, showing how the eggs are sorted by number and then the eggs of each hen are placed in separate hatching baskets, which are carefully numbered and securely fastened. At the bottom, a hatching sack has been used to keep one hen's eggs and chicks hatching from them separate from those of other hens. By carrying on pedigree breeding work the poultry breeder is able to select progeny for future breeding purposes produced by dams whose eggs gave high hatchability. (U. S. D. A.)

White Leghorns had a higher specific gravity than the eggs of his Barred Plymouth Rocks. It was found that White Leghorn eggs with a specific gravity of 1.078 or better had a hatchability of 85.9 per cent and those with a specific gravity of 1.072 or lower had a hatchability of 50.9 per cent. Using the same division point in Barred Plymouth Rock eggs, the hatchability for each group was 87.3 and 55.7 per cent, respectively.

Interior Egg Quality and Hatchability. It has been determined that certain internal egg qualities have a direct bearing upon hatchability, although for the most part the relationship has not been demonstrated to be hereditary. That the amount of proteins and fats in eggs apparently does not influence hatchability has been shown by Cross (1912). The amount of solids in the yolk do not affect hatchability, as shown by Bronkhorst (1933) and Bronkhorst and Hall (1935). On the other hand, the vitamin A content of the yolk apparently influences hatchability, as shown by the work of Barancheev (1936), who secured a much higher hatchability of eggs containing deep yellow yolks than of eggs with pale yellow yolks, the intensity of yellow color being an index of the relative amount of vitamin A precursors present. From several lines of nutritional investigations, it has been shown that the vitamin D content of yolks influences hatchability, but it has not been determined that hens may differ with respect to the efficiency with which vitamin D is utilized.

That the condition of thick white in eggs may influence hatchability was indicated by the results secured by Van Wagenen (1935), Van Wagenen and Hall (1936) and Hall and Van Wagenen (1936), the condition of thick white having been determined by a scoring method. The eggs from the strain of birds having a high-quality score hatched considerably better than the eggs from the strain of birds having a low-quality score.

Godfrey (1936) found that the less total albumen there is in an egg the higher the hatchability and the less the amount of thick albumen in an egg the higher the hatchability in general. At the same time, the results of Godfrey (1936) and Hall and Van Wagenen (1936) show that the percentage of thick white is not related to hatchability. Rudy and Marble (1939) conducted a two-year investigation of the relationship between interior egg quality and hatchability and found that in the first year the only character significantly related to hatchability was the percentage of thick white in total white, but in the second year not even this character was related to hatchability. Heiman (1939) found that neither the albumen index nor the albumen height was associated with hatchability.

Embryo Malposition and Hatchability. The normal position of the embryo at hatching time is with the head toward the larger end of the egg and with the neck bent sufficiently to bring the head to the right side of the body and the beak under the right wing, the tip of the beak pointing toward the air cell; the legs are on the ventral side of the embryo with the feet folded so that the toes reach the head.

It has been found, however, that embryos sometimes assume modifications of the normal position, usually without materially affecting hatchability though occasionally very definitely so. Sanctuary (1925) found that 51.7 per cent of 1,490 embryos that died during the incubation period preceding hatchability showed some form of malposition. Comparable data by Hutt (1928–29) showed 55.85 per cent malposition embryos. From the data of Hutt (1928–29), Byerly (1930), Hale (1930), Smith (1930), Hutt and Cavers (1931), Upp (1934), and Dove (1935), the various malpositions may be described briefly as follows:

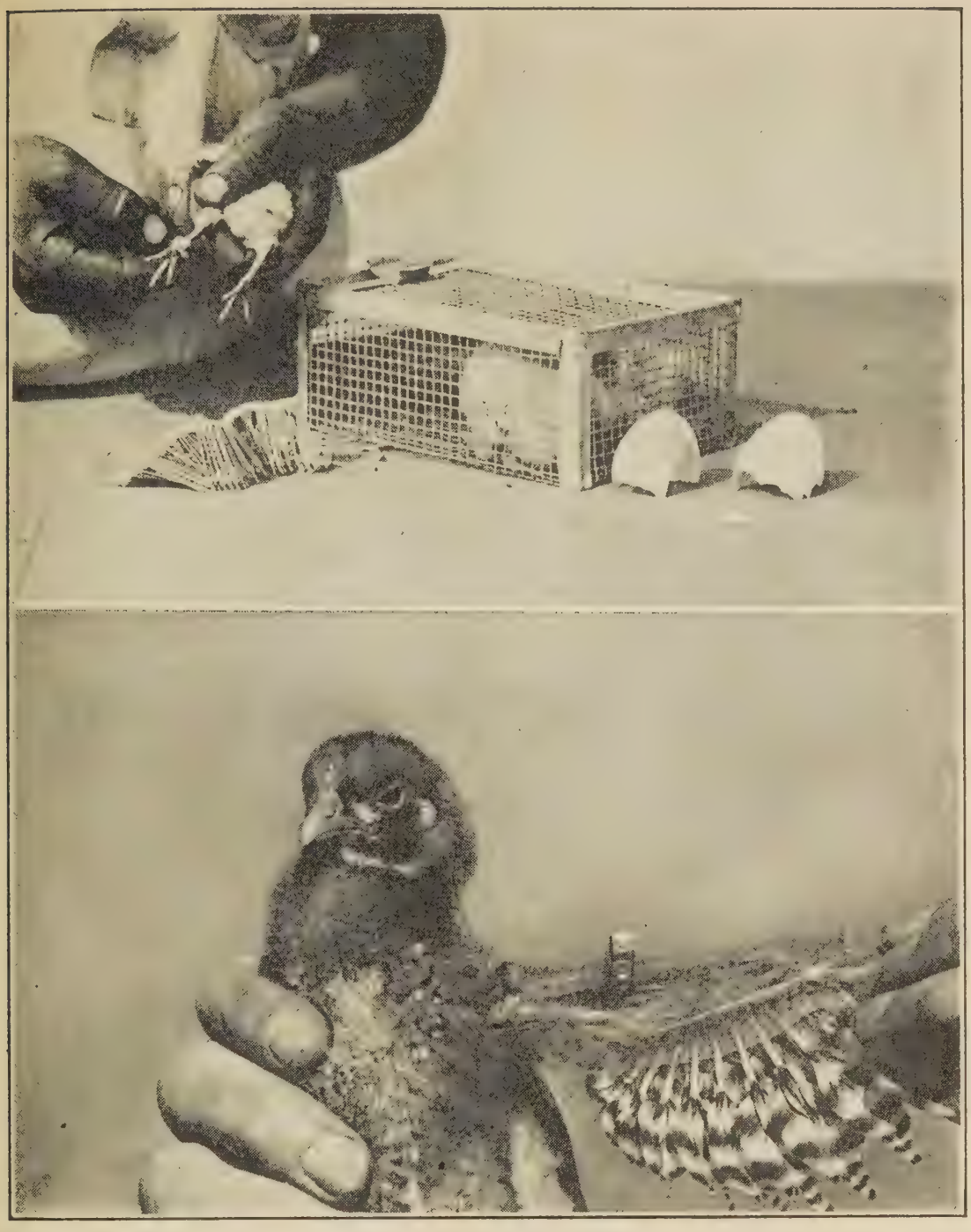
1. Head extends down median line, buried between the thighs.
2. Head in the small end of the egg.
3. Head turned to the left, beak pointing opposite air cell.
4. Head rotated so that beak points away from air cell.
5. Both feet are placed on top of the head.
6. Beak over right wing.

As Landauer (1937) points out, it is generally recognized that factors giving rise to delay in the development of the embryo are an important cause of embryo malformations. At the same time, Byerly (1932) and others have suggested that one or more of the malpositions may have a genetic basis. Byerly (1930) concluded that the frequency of teratological abnormalities is reduced by crossbreeding. For a general review of the literature on malpositions, the reader is referred to Byerly (1930), Byerly and Olsen (1931, 1933, 1934*a*, 1934*b*, 1936, and 1937), Dove (1935), Hutt (1938), Hutt and Cavers (1931), Hutt and Pilkey (1929–30), North (1938), Olsen and Byerly (1935), Taylor (1932), Upp (1934), and Waters (1935*a*, 1935*b*).

The occurrence of teratological monsters among embryos lowers hatchability. Reference should be made to such papers as those of Chidester (1927), Hutt (1930), Landauer (1937), and Komi and Nakamura (1938), which contains a good review and several new cases.

Laying Traits and Hatchability. There are two laying traits that have been shown to influence hatchability, the first being the time of day that eggs are laid and the second being the time interval between layings.

Results were secured by Hutt and Pilkey (1929–30) during the



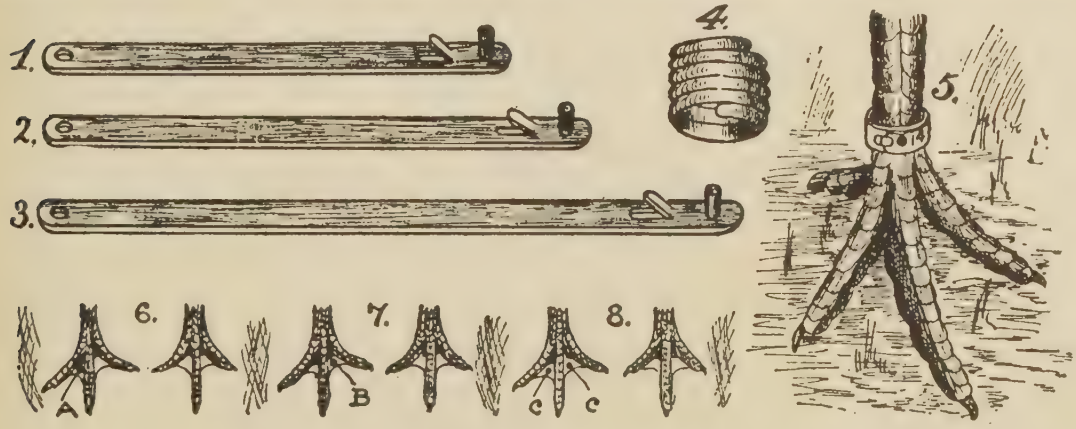


FIG. 62. At the top, leg banding the chicks. In the center, wing band in place. At the bottom, wing and leg bands of various kinds; also various ways of toe-punching. Banding the chicks makes possible the identification of superior families. (U. S. D. A.)

early spring season which indicated that eggs laid in the morning, especially those laid before 9 A.M., hatched better than eggs laid in the afternoons. Relatively more teratological monsters were observed in eggs laid in the afternoon as compared with eggs laid in the morning. It was assumed that better hatchability of the morning eggs was in part due to the fact that some of them had been held in the bird's body a sufficient length of time to have passed the stage when chilling of the eggs would otherwise have killed the developing embryos.

Although the results secured by Nicolaides (1933) showed that, on the whole, morning eggs hatched better than afternoon eggs, it was also observed that eggs laid between 7 and 9 A.M. did not hatch as well as eggs laid between 9 A.M. and noon. Hays (1936) found that the hour of the day at which eggs were laid had no influence on their hatchability, whereas Funk (1934) concluded from a large number of observations that the hatchability of eggs laid in the afternoon was slightly better than that of eggs laid in the morning. McNally and Byerly (1936) also observed a slightly higher hatchability among eggs laid late in the day than among morning eggs. The best hatchability was obtained in eggs that required approximately 27 hours between successive eggs. Funk (1939) found that the order of eggs within a clutch has no bearing on hatchability but that eggs laid in multiple clutches tend to hatch better than eggs laid in single-egg clutches.

Egg Production and Hatchability. Some poultrymen are of the opinion that heavy egg production prior to the breeding season tends to reduce hatchability, whereas other poultrymen believe that heavy egg production during the breeding season tends to reduce hatchability. Evidence secured on these two points shows that neither opinion is well founded, except perhaps in the case of late-hatched pullets that have been "forced" into heavy production through heavy feeding and the excessive use of artificial lights.

Lamson and Card (1920), using White Leghorns, observed that the number of eggs laid during the 90 days prior to the hatching season did not affect hatchability. Knox (1927) also obtained no correlation between antecedent egg production and hatchability. Atwood (1927) found that heavy feeding of the breeding hens to induce heavy egg production prior to and during the hatching season did not adversely affect the hatchability of the eggs produced. Jull (1928) found that in Barred Plymouth Rocks, Rhode Island Reds, and Single-Comb White Leghorns, egg production prior to the breeding season did not affect hatchability. Martin and Insko (1930) found the same to be true in the White Leghorns and Barred Plymouth Rocks with which

they worked. It is apparent, therefore, that the number of eggs laid prior to the hatching season has no effect on hatchability.

The relationship between current egg production, the number of eggs laid during the hatching season, and hatchability has been but recently investigated. Heuser (1927) observed that eggs from hens laying very heavily did not hatch as well as eggs from hens laying only moderately during the hatching season. Should such a situation exist among all flocks it would be unfortunate, inasmuch as high annual egg production is correlated with high monthly as well as high spring egg production.

Byerly, Titus, and Ellis (1933), from data secured from several pens of Rhode Island Red pullets and cockerels, the cockerels being shifted from pen to pen daily, obtained a positive correlation of 0.16 ± 0.036 between intensity of egg production and hatchability. This low, though significant, correlation was obtained on the basis of average intensity and average hatchability of pullets in different pens, each of which was on a diet differing in protein level. With the percentage of protein in the diet held constant, the net correlation between hatchability and intensity of production was 0.18 ± 0.036. This correlation indicates that relatively heavy egg production during the breeding season did not reduce hatchability.

Intensity of egg production during March and April when compared with hatchability for the same two months gave a positive correlation of 0.23 ± 0.27. This significant correlation was secured with pullets on different diets. With pullets on the same diet, Byerly, Titus, and Ellis secured a positive correlation of 0.30 ± 0.041. This correlation is significant, and the authors were led to conclude "that hens able to lay eggs at a high rate on a particular diet will, in general, produce a higher percentage of hatchable eggs than those able to lay only at a low rate on the same diet."

Data bearing on this point from flocks of yearling and older Barred Plymouth Rocks, Rhode Island Reds, and Single-Comb White Leghorns have been presented by Jull (1931), whose results are given in Table 55. In the compilation of the data the influence of the male on hatchability was eliminated by dividing the females in each breeding pen into two groups, according to whether each female was above or below the mean percentage of hatchability of all females in the pen. Data on egg production covered the 50-day breeding season.

Regarding the data in Table 55, it is shown that in the case of each breed the mean egg production of the group showing hatchability above the mean percentage of hatchability of the females of each pen is higher in every case than in the group showing hatchability below

TABLE 55. CURRENT EGG PRODUCTION IN RELATION TO HATCHABILITY
(Jull, 1931)

Breed	Mean Current Egg Production per Pen of Group Showing Hatchability *above* Mean Per Cent Hatchability of the Females of Each Pen	Mean Current Egg Production per Pen of Group Showing Hatchability *below* Mean Per Cent Hatchability of the Females of Each Pen
Barred Plymouth Rock..	23.5 ± 0.7	21.7 ± 0.6
Rhode Island Red.....	25.0 ± 0.3	23.6 ± 0.3
White Leghorns.....	25.9 ± 0.3	24.4 ± 0.3

the mean percentage of hatchability of the females of each pen. The difference in mean egg production is significant in the case of Rhode Island Reds and White Leghorns, showing that heavy egg production during the breeding season is not detrimental to, but apparently conducive to, good hatchability. Similar results have been reported by Funk (1934) and von Andra (1938). It is possible to conclude, therefore, that a program of breeding for high hatchability can be carried on simultaneously with a program of breeding for high egg production.

Breeding to Increase Hatchability. Since hatchability is inherited, as pointed out in Chapter VI, it is obvious that the hatchability of a flock can be increased by the proper selection of the males and females placed in the breeding pens.

The poultry breeder should keep an accurate record of the hatching results secured from each female and each male and should eliminate from future breeding pens all birds that have been shown to carry lethal genes, which cause the death of embryos, and all birds that have been shown to produce abnormalities. The eggs should be gathered from the nests as soon as possible after being laid, held for incubation at a temperature of approximately 50° F., and incubated properly so as to reduce the number of malpositions and malformations to the minimum. The breeders should be tested for pullorum disease and all carriers of the disease removed from the breeding pens. Too close inbreeding should be avoided.

Females that gave poor hatchability results when used as breeders the first time should not be used again. Hyre and Hall (1932) divided a flock of Single-Comb White Leghorns into three pens according to the hatchability results secured from them the first year that they were first used as breeders. The first pen comprised birds that, on the

basis of the first year, gave low hatchability; the second, birds that gave medium hatchability; and the third, birds that gave high hatchability. When the pens were bred from the second year, the first pen gave a hatchability of 15.9 per cent, the second pen 55.1 per cent, and the third pen 75.1 per cent, these results being based on six or more hatches from each pen.

Since hatchability is inherited, the breeders used each year should be selected from dams that gave approximately 75 per cent hatchability. If the policy is adopted of selecting each year only those birds for breeding purposes whose dams gave high hatchability, the poultry breeder should be able to improve the hatchability of his flock quite materially.

The hatchability of eggs is of very great economic importance to the poultry industry as well as to the 12,000 breeder and commercial hatcheries in the United States. These hatcheries have an egg capacity of over 300,000,000 eggs, and it is safe to assume that over one billion eggs are set annually, of which approximately 30 per cent, or 300,000,000, fail to hatch.

TABLE 56. EGG COST PER CHICK IN RELATION TO HATCHING PERCENTAGE

(Carver and Buchanan, 1926)

Hatchery Number	Eggs Set	Chicks Hatched	Per Cent Hatch	Egg Cost per Chick, Cents
1	49,117	25,365	52.0	8.1
2	273,200	154,950	57.0	7.4
3	115,200	68,000	59.0	7.1
4	378,000	223,000	60.0	6.8
5	40,318	25,100	62.0	6.7
6	16,000	10,000	62.5	6.7
7	24,500	18,000	73.0	5.7
8	29,000	22,000	76.0	5.5

In a two-year survey of the hatchery industry of Maryland, Poffenberger and DeVault (1939) found that the cost of hatching eggs represented 63.7 per cent of the total cost of producing day-old chicks and that there was a direct relationship between the hatchability of the eggs and profit in operating a hatchery. Among the most profitable hatcheries, the hatchability was 72.6 per cent; among the least profitable hatcheries, it was 67.2 per cent.

The egg cost per chick is affected by the hatching percentage secured, as shown by the data submitted by Carver and Buchanan (1926).

Since egg costs constitute the most important single cost factor in hatching, and since the hatchability of eggs is such an important factor in determining the egg cost per chick, it is interesting to ascertain the relationship that exists between the premium paid for hatching eggs and their hatchability. Most hatcheries pay a premium above market price, the amount of the premium differing greatly and depending upon the extent to which flock-improvement work is carried on among the flocks producing the eggs for the hatchery.

The chart shown in Fig. 63 may be used for calculating the egg cost per 100 chicks when the per cent of salable chicks hatched and the cost of the eggs in cents per dozen are known. The range in hatchability is indicated by the vertical line at the left side of the chart, the line being graduated from 100 at the bottom to 0 at the top. The range in price paid for eggs in cents per dozen is indicated by the vertical line at the right side of the chart, the line being graduated from 0 at the bottom to 100 at the top. The diagonal line extending between the 0 points of the two vertical lines is graduated from 1 to 50 and indicates the egg cost per 100 chicks expressed in terms of dollars per 100 chicks.

Placing a ruler across the chart and crossing the vertical lines at the right and left sides at the appropriate price per dozen for eggs and the appropriate per cent hatch of salable chicks gives the egg cost per 100 chicks on the diagonal line. If hatching eggs cost 48 cents per dozen and 78 per cent of them hatch into salable chicks, the egg cost per 100 chicks is $5; but, if 45 per cent hatch into salable chicks, the egg cost per hundred chicks is $8.

This chart may also be used to compute the premium, over the market price, that the hatchery operator can afford to pay for eggs. He knows the selling price of his chicks and should know the required overhead and profit to be charged to each 100 chicks. Suppose that chicks sell for $10 per 100, that the hatchery operator required a profit of $2 per 100 chicks, and that his overhead amounts to $3 per 100 sold. This leaves $5 per 100 as the permissible egg cost per 100 chicks. By placing the edge of the ruler at the $5 point on the diagonal line and also at the point on the line at the left side representing the per cent hatch obtained, the price the hatchery operator can afford to pay for eggs will be read at the point at which the edge of the ruler intersects the line on the right side. The difference between this price and the market price of eggs is the premium that the hatchery operator can afford to pay.

Many breeders and hatchery operators are faced with the problem of determining the price they should pay for male birds of superior

breeding worth. The chart shown in Fig. 64 has been designed to assist in determining the relationship among the three factors: salable chicks hatched per male, the value of the male, and the premium in cents per chick. This second chart was constructed so that the vertical line on the left is graduated to indicate salable chicks sired by a male; the

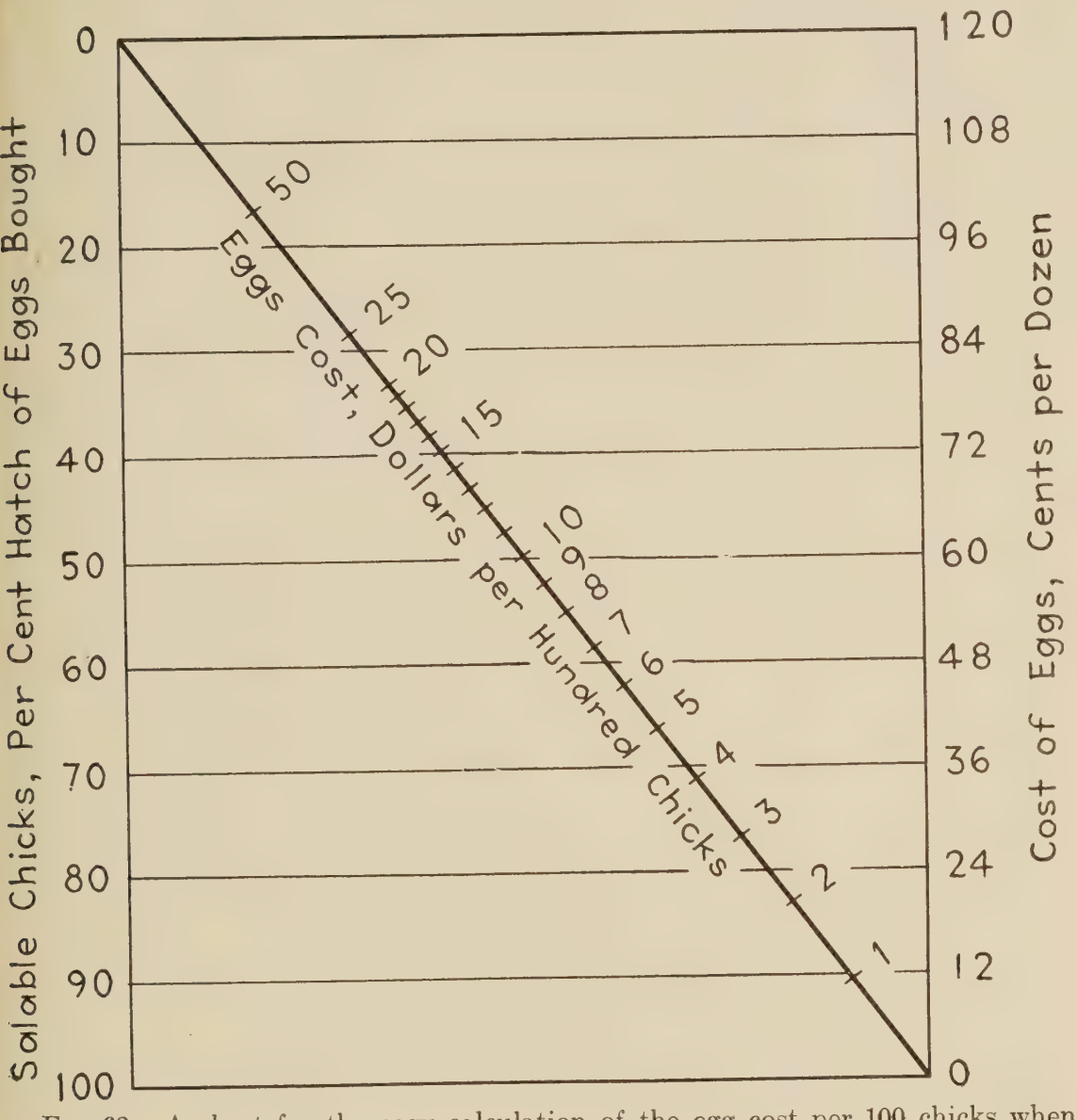


FIG. 63. A chart for the easy calculation of the egg cost per 100 chicks when the percentage of salable chicks hatched and the cost of eggs in cents per dozen are known. (Byerly, 1936.)

diagonal line graduated to show the premium obtained because of the use of the male, expressed in cents per chick; and the vertical line on the right to show value of the male in dollars. Given any two of the three values just stated, it is possible to obtain the third by placing the edge of a ruler through the two known values; the third may then be read directly.

Both charts may be used to supplement each other in determining

the influence of hatchability, for the number of salable chicks produced is obviously greatly affected by hatchability, and the premium that may be paid on eggs bought depends directly on hatchability. If a premium of $4 per 100 chicks is obtained through the use of superior

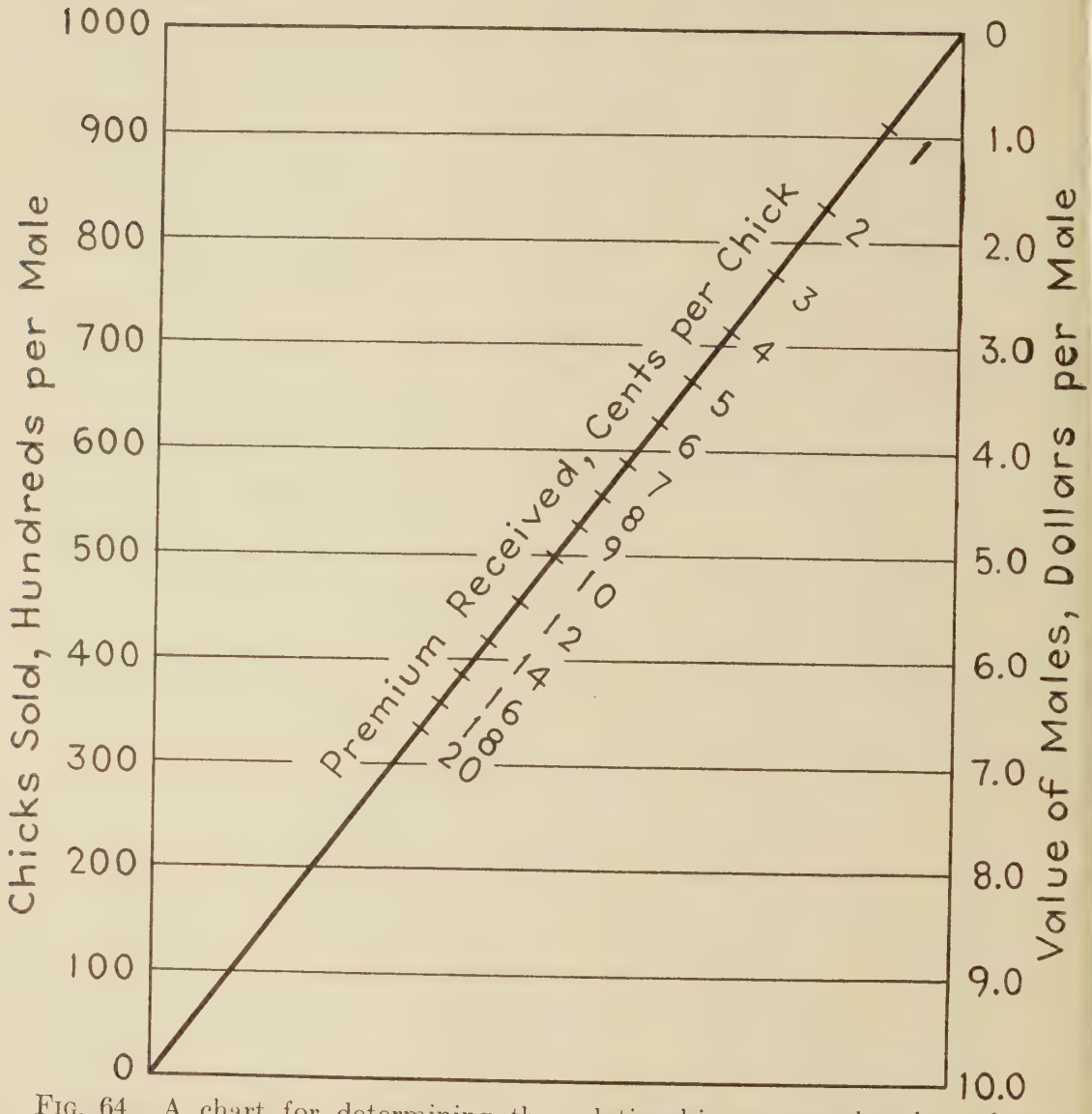


FIG. 64. A chart for determining the relationship among the three factors, salable chicks hatched per male, the value of the male breeders in dollars, and the premium in cents per chick. (Byerly, 1936.)

males, then this value may be substituted on the diagonal line of the first chart for the $4 point for egg cost of chicks; and by passing the straightedge through this point and through the point representing the hatchability obtained, the premium that may be paid per dozen eggs is read directly on the vertical line at the right of the chart. For example, if the hatchability was 70 per cent, then a premium of about 34 cents per dozen may be paid for the use of the superior male. The charts in Figs. 63 and 64 should be invaluable to hatcherymen.

BREEDING FOR VIABILITY

There is little point in breeding poultry for any particular purpose if mortality decimates the flock and eliminates profits. Losses from mortality have become of paramount importance in the poultry industry of the United States as well as of other countries. Some of the mortality that occurs in chick and adult flocks is due to environmental factors, including faulty diets and mismanagement. Such mortality may justly be charged up to the negligence of the poultry operator, for most of it is avoidable. On the other hand, a great deal of the mortality that occurs is due to lack of ability on the part of the chicken to withstand the ravages of the organisms of disease, the organisms of several diseases being ever present on practically every poultry plant.

Contaminated soil on which poultry is ranged year after year gives rise to an increase in the eggs of parasites and organisms of disease with which birds have to contend. Overcrowding chick and laying houses tends to lower the physiological resistance to disease the birds may possess. The normal traffic that occurs in shipping market poultry, breeding stock, hatching eggs, and baby chicks tends to spread disease organisms over the country. Wild birds, predatory animals, and even winds may spread disease. These and various other hazards make it necessary for the chicken to possess a strong constitution if it is to be expected to live long enough to fulfill the purpose for which it was intended.

Diseases are generally classified as noninfectious and infectious, depending upon whether or not a pathogenic organism is present. Since losses from infectious diseases are of such serious consequences to the poultry industry and since it has already been shown in Chapter VI that resistance to certain specific diseases is hereditary, it is important to develop by the adoption of proper breeding methods stocks that have the inherited capacity to resist disease. Although some progress has been made in developing strains of birds that show a relatively high degree of resistance to one or more specific diseases, the fact should be appreciated that such strains may be highly susceptible to various other diseases. Thus it becomes clear that the problem of breeding for viability is an extremely complicated one.

Chick Viability. Very little is known concerning the possibilities of breeding for viability in chicks because practically no experimental work has been done along this line. Experience has indicated that during the past decade growing chick mortality has tended to decline to some extent, apparently largely as the result of improved manage-

ment practices. Records of performance breeders who carry on pedigree breeding work and record the mortality that occurs during the growing season among the progeny of each dam have long since learned that there are sometimes marked differences in mortality among different families of growing chicks. Farmers and commercial poultrymen have often noted marked differences between the mortality rate of the chicks secured from two different strains of breeding stock, even when the two strains of chicks are reared under identical environmental conditions.

Differential viability was found to exist among strains of chicks reared under identically the same environmental conditions and fed the same diets but secured from different strains entered in the Nebraska flock-testing project in 1935. In some strains of heavy breeds, the viability of chicks during the first four weeks was as high as 87 per cent and in other strains as low as 30 per cent. Among Leghorn chicks, the first-four-week viability among strains ranged from 99 to 69 per cent.

A few records will suffice to demonstrate the differences that sometimes occur in the viability of the progeny of different sires. Jull (1934) has reported a viability of 95.7 per cent up to four weeks of age among chicks produced by 14 Rhode Island Red sires, but, among these sires, the viability of their progenies varied from 100 per cent to approximately 88 per cent. Jull (1935) has also reported other data on differences in the viability to four weeks of age of the chicks of different sires, one having chicks with a viability of 97.9 per cent and another having chicks with a viability of 88.6 per cent. It should be noted that these different families of chicks were reared under the same environmental conditions.

Marble (1939) has shown that certain White Leghorn and Barred Plymouth Rock sires differed greatly from other sires of the same respective breeds with regard to the viability of their progeny, and that, by breeding from families showing high viability, it was possible to increase considerably over a five-year period the viability of all the chicks and laying pullets. Bearse, McClary, and Miller (1939) showed that, as the result of eight years of breeding two strains of White Leghorns, the progeny of one strain was found to be more resistant to disease than the progeny of the other strain, the pullet-rearing viability being 74.7 and 68.0 per cent, respectively. Bostian and Dearstyne (1939) have shown that differences existed among families of White Leghorns with respect to progeny viability. For a period of 500 days from hatching time some families showed 100 per cent viability, whereas other families showed less than 70 per cent viability.

Although resistance to a certain specific disease has been demon-

strated to be inherited, the influence of environment must always be taken into consideration in developing a plan to breed for resistance to a disease. Resistance to pullorum disease is inherited, as pointed out in Chapter VI and confirmed by Quigley and De Volt (1940), but Roberts, Severens, and Card (1939) have observed that environment may sometimes exercise a profound influence on the hereditary nature of resistance. In their research on the genetics of resistance to pullorum disease, it was discovered after a change of diet that abnormally high mortality occurred among the "control" pens of chicks that had not been inoculated, and it was impossible to secure evidence that they had been accidentally inoculated. Restitution of the normal diet resulted in restoring the mortality to normal.

The normal course of procedure in combating pullorum disease has been to test the breeding stock to determine the presence or absence of the causative organism, *Salmonella pullorum*. Although this biological test is not claimed to be 100 per cent accurate, the repeated application of the test under proper conditions by properly qualified persons has served to reduce losses to the minimum among chicks hatched from the "noncarriers." Pullorum disease is not inherited, as are plumage color and egg production, and, since the causative organism becomes localized, for the most part, in the ovary of the female, the causative organism is transferred from the female to her chick progeny through the medium of the egg. It might be supposed that testing to remove all "carriers" of the organism would solve the problem of combating the ravages of pullorum disease among chicks.

That such is not necessarily the case, however, has been demonstrated by the work of Quigley and De Volt (1940). They procured chicks from breeders whose flocks were shown, by test, to be "free" of pullorum disease for several years and found that when such chicks were inoculated with the pullorum organism the mortality was usually very high, much higher than among their own chicks whose parents had been bred for resistance to the disease. The results of these observations would seem to indicate that although the testing program may eliminate the "reactors" or carriers of the organism that causes the disease, it may not eliminate the birds that are themselves susceptible and that produce chicks susceptible to the disease. Many farmers and commercial poultrymen who purchase chicks from "pullorum-free" flocks and raise them with chicks hatched from breeding stock that has not been proved to be free of the disease have found that the mortality among the pullorum-free chicks is often much greater than among the other chicks. The pullorum-free chicks are apparently much more susceptible to the disease than the chicks

secured from parents from which the disease had not been entirely eliminated.

These comments are in no wise to be considered as condemnation of the testing program but rather to emphasize the importance on the part of those who have their flocks tested annually, or more frequently, of adopting a program of breeding to develop strains of breeding stock resistant to pullorum disease. It is obvious, of course, that until such pullorum resistant strains are established, the testing program to eliminate breeders which harbor the organism must be carried on as the most practicable procedure in eradicating losses in chick mortality which would otherwise occur.

Another case may be cited to illustrate the relationship between the incidence of mortality among chicks and the environmental conditions under which they are kept. Fraser (1937–38) has stated that among the Brown Leghorns maintained at the University of Edinburgh mortality was quite low and that since 1928 no case of fowl paralysis had been observed. In 1937, hatching eggs from this stock were sent to the Rowett Institute where a severe outbreak of fowl paralysis occurred among White Leghorns in 1934. The mortality up to December 20 among the University chickens was 63.6 per cent in contrast with 54.8 per cent among the Institute chickens. The University stock proved highly susceptible to fowl paralysis when exposed to the disease.

The foregoing discussion on the methods of combating the ravages of disease brings to the fore the fundamental principles involved in breeding for chick viability. As Lambert (1935) has pointed out, there are three possible methods of disease prevention available to poultrymen. The first, and, as he has said, the most important, is proper hygiene and sanitation; the second is through the use of various therapeutic agents, designed to "cure" the disease; and third is the genetic method, or breeding for resistance to disease.

Up to the present, it would seem that the reduction that has occurred during about the past decade in growing-chick mortality has been accomplished largely through improved hygienic and sanitary methods that have been adopted. The real problem facing poultry raisers is not so much knowing how to combat or control disease as knowing how to prevent disease from making its appearance. Curing sick chickens by the use of therapeutic agents will probably never help the poultry industry very much, for the simple reason that birds that are susceptible to various diseases will remain in the flock to perpetuate susceptibility to the disease. The obligation rests upon the flock owner to assist the chicken in every way possible in main-

taining or even improving the defensive mechanism against the invasions of disease-inducing organisms. The results of various breeding tests have shown that it is possible to improve chick viability by applying the progeny test in the selection of breeding stock. Knox (1939) has pointed out that the mass mating of males and females that have survived a severe outbreak of disease gives little promise of developing a strain possessing a high degree of viability.

From the practical standpoint it is imperative that the poultry breeder who carries on pedigree breeding work should keep accurate records of the mortality among the growing chicks secured from each female breeder as well as from each male breeder. The female and male breeder whose progeny shows a low degree of viability should be discarded and their progeny should also be rejected in the selection of future breeders. The farmer and commercial poultryman who do not practice pedigree breeding would be well advised to secure chicks or breeding stock from poultry breeders who have demonstrated that they have strains of birds whose chicks are noted for their viability when exposed to disease.

Adult Viability. Conditions in the poultry industry in the United States and some other countries have become such that losses from adult mortality is the most important single factor affecting financial returns. Adult mortality has driven many poultrymen out of business and has crippled the breeding plans of many poultry breeders. Results have been secured, however, which indicate that it should be possible to reduce losses from adult mortality quite materially by the adoption of a certain line of breeding procedure.

In Chapter VI, it has been shown that strains may differ with respect to their ability to resist the invasions of the organisms of a specific disease and that resistance to a specific disease is hereditary in nature. The next logical step would seem to be to determine whether or not it is possible to develop strains that are inherently resistant to disease in general.

From an analysis of viability data in the Suffolk laying trials in England from 1930 to 1935, inclusive, it was observed that, among the birds entered by 20 different poultry breeders, the birds entered by 12 poultry breeders had a viability of 93 per cent, whereas the birds entered by the other 8 poultry breeders had a viability of 80 per cent. Among 7 White Leghorn sires that had 50 or more pullets each that were put in the laying house, Jull (1934) observed that the first-laying-year viability varied from 92 per cent in one family to 74 per cent in another family. The first-laying-year viability of the

progeny of Rhode Island Red sires was reported by Jull (1935) to vary from 94.5 to 80.0 per cent.

The fact that the steady increase in laying pullet mortality that has occurred from year to year during about the past fifteen years is not necessarily influenced by the level of egg production attained is clearly indicated by data submitted by Platt (1936), Hutt (1938), and

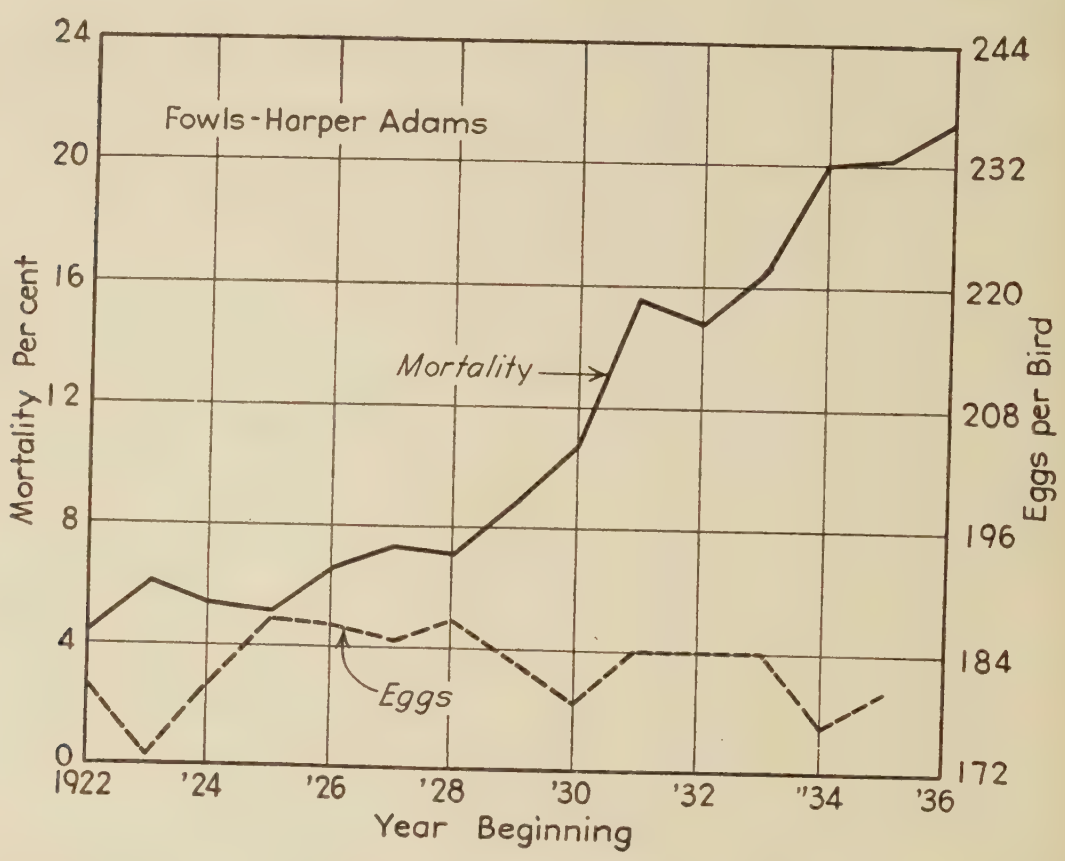


Fig. 65. Average egg production and mortality during 48 weeks among pullets entered in laying trials from 1922–23 to 1936–37 at Harper Adams Agricultural College, Newport, Salop, England. (Hutt, 1938.)

Ferguson (1938). Platt showed that among White Leghorns entered in the Vineland Egg Laying contests from 1918 to 1933, inclusive, the mortality during the first three years varied from 6.48 to 11.25 per cent, whereas during the last three years the mortality varied from 21.78 to 25.99 per cent. By comparison, the percentage of egg production during the first three years varied from 44.82 to 52.95 and during the last three years, from 55.18 to 57.18. The observations of Hutt and Ferguson are shown in graphic form in Figs. 65 and 66, respectively. Hutt's data were obtained from the records of the English National Laying Trials conducted at the Harper Adams Agricultural College in England. Ferguson's data were obtained from the records of farm demonstration flocks in Ohio.

The observations of Platt (1936), Hutt (1938), and Ferguson (1938) show that over a period of years laying-pullet mortality has increased out of all proportion to any increase in egg production per bird. Not only has the loss of dead birds become a very serious menace to the poultry industry, but there must also be taken into consideration the effects of an invasion of disease on the egg production of laying pullets that subsequently die as well as those that live. Harris (1926, 1927) analyzed the records of egg production among 4,678 White Leghorns, 1,784 Rhode Island Reds, and 967 White Wyandottes and found that the average egg production of birds which subsequently died was lower during comparable periods than that of birds which survived. Dudley (1928) questioned the significance of the differences which

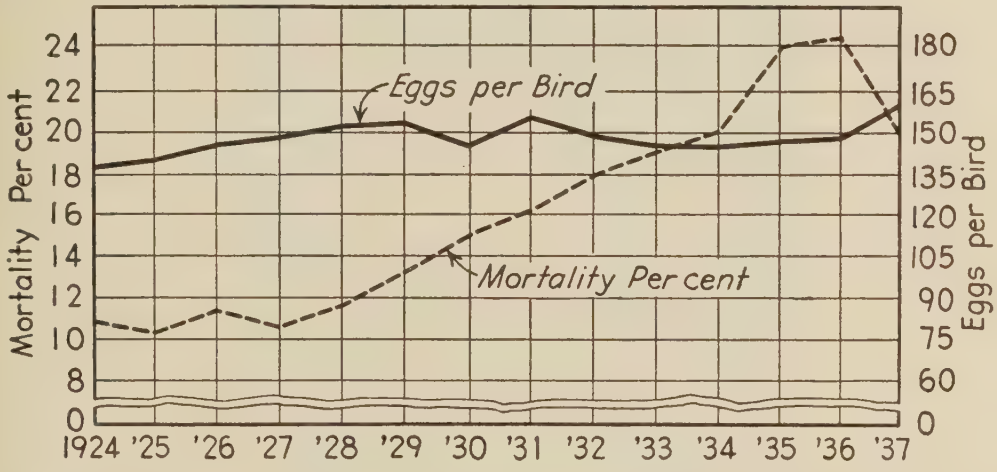


FIG. 66. Average egg production per bird and mortality of laying birds on Ohio poultry record forms, 1924–37. (Ferguson, 1938.)

Harris observed although the following workers also found that birds which died were poorer layers during their production period than were birds which survived: von Eickel and Kruger (1933), Jull (1934), and Weaver and Bird (1934). Lerner, Taylor, and Lubbehusen (1939) observed that within each sire's progeny the pullets with relatively low egg production records are more likely to die during the first laying year than those with higher records. In addition to this, Bird (1939) observed that egg production is lowered among the survivors in a flock invaded by disease. Marble (1939) observed that birds which died during the fore part of their first laying year laid at a lower rate than birds which did not die and that birds which died toward the end of their first laying year accumulated a lag in production which resulted in distinctly lower levels of egg production than among birds which survived throughout their first laying year. Munro (1936), Bird (1939), and Clark (1940) concluded that breeding for high egg production is compatible with breeding for viability.

In order to reduce the high annual costs of flock replacements made necessary because of excessive laying-pullet mortality, it would be highly desirable to be able to keep the first-year survivors for as many years as egg production is maintained at a satisfactory level. It has already been shown in Chapter VII that second-year production may vary from about 72 to about 88 per cent of first-year egg production, depending to some extent upon the level of first-year egg production. After the second-laying year, the decline in egg production is usually

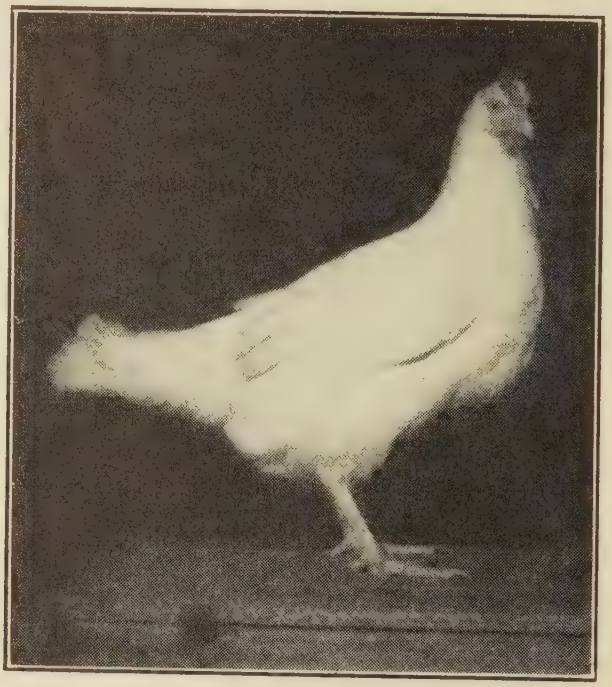


FIG. 67. A very good record of sustained production. This Cornell University Leghorn laid 1,515 eggs over a period of 8 years. (Hall, 1938.)

greater so that very few birds produce profitably after they are four or five years old. On the other hand, birds that live that long or longer may prove to be extremely valuable breeders even if they lay but few eggs during the breeding season. Such birds have demonstrated at least that they had the ability to resist the organisms of diseases that are usually present on most poultry plants. A number of private breeders and some of the state experiment stations have secured individual records of egg production of over 1,300 eggs. In Table 57 are given the records of some state experiment station birds, together with the approximate age of the bird at the time the record was made, the data having been supplied by Martin (1940).

It is to be hoped that the time will soon come when poultry breeders will give much more consideration to the importance of breeding for sustained production over a period of years. The results which Green-

TABLE 57. LONGEVITY RECORDS OF EGG PRODUCTION
(Martin, 1940)

No. Eggs	Age	Breed	Station
1,515	8	White Leghorn	Cornell University
1,504	7	White Leghorn	Iowa Exp. Station
1,487	7	White Leghorn	Ky. Exp. Station
1,475	8	White Leghorn	Ky. Exp. Station
1,472	9	White Leghorn	Iowa Exp. Station
1,421	10	White Leghorn	Purdue University
1,335	9	Oregon	Ore. Exp. Station
1,333	8	White Leghorn	Wis. Exp. Station
1,325	8	White Leghorn	Utah Exp. Station
1,316	10	White Leghorn	Mo. Exp. Station

wood (1937) secured led him to conclude that sustained egg production and viability may be bred into a flock. Clark (1930) reported that in an original flock of 200 White Leghorns in which no culling was practiced over one-half of them lived through 6 years and 26 lived through 10 years.

Hutt (1938) has pointed out that by far the major portion of the laying-pullet mortality that occurs is due to diseases that are not entirely amenable to sanitation, immunization, and the elimination of carriers and exposed birds. Among 1,922 mortalities that occurred among birds entered in two New York State laying contests from 1931 to 1937, inclusive, it was found that fowl paralysis (a general term including leucosis, lymphocytoma, neurolymphomatosis, tumors, and related conditions) was responsible for 38.4 per cent of the total mortality, diseases of the reproductive system 25.3 per cent, and prolapse of the oviduct 11.2 per cent. The 1935 report of the director of the Storrs Agricultural Experiment Station contains a tabular statement of the causes of 318 deaths among 1,300 birds entered in the Storrs Egg Laying Contest in 1934 and shows that fowl paralysis, diseases of the reproductive system, and kidney diseases were the principal causes of the 24.5 per cent of mortality that occurred. Other experiment station reports have contained similar observations.

On the other hand, Beach (1939) has shown quite clearly that the major portion of adult mortality may be unrelated to infection, parasitism, or disease of an otherwise specific nature. Careful autopsy records were kept of all chickens over six months old that died or were

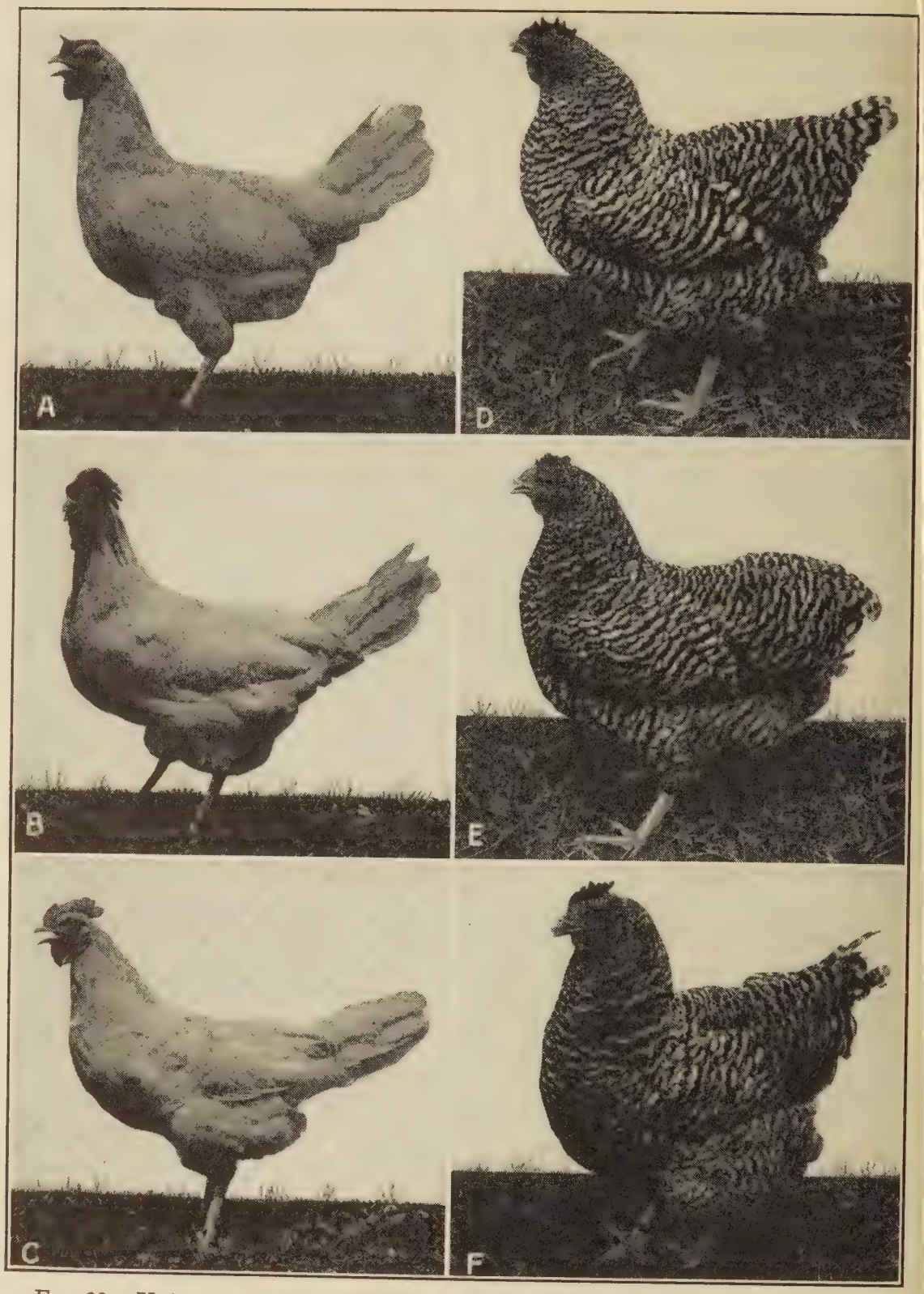


FIG. 68. University of Wisconsin White Leghorns and Barred Plymouth Rocks noted for good records over a period of years. Top left laid 1,333 eggs in 8 years and hatchability was 89 per cent. Below her are two nieces that laid 1,366 and 1,320 eggs, respectively, in 8 years and their hatchability was 77 and 87 per cent. Top right laid 940 eggs in 6 years and hatchability was 78 per cent. Below her are two daughters that laid 993 eggs in 7 years and 810 eggs in 5 years, respectively, and their hatchability was 58 and 86 per cent, respectively. (Photo and records by Holmes.)

removed as culls from the University of California Poultry Department flock for a period of four years and of all adult chickens that died among the flocks of seven commercial poultrymen for a period of 19 months. From the autopsy records of 7,771 birds it was revealed that 62.5 per cent of the Poultry Department flock that died, 50.8 per cent of the Poultry Department flock that was culled, and 53.4 per cent of the mortality of the commercial flocks were due to nonspecific disease conditions.

Specific diseases, particularly lymphomatosis, intestinal coccidiosis, and coryza were primarily responsible for the mortality that occurred during the first laying year but thereafter were relatively insignificant. Beach has pointed out that the autopsy records of the Poultry Department birds that were culled because of unsatisfactory egg production records showed that approximately one-third of them had pathological changes involving the reproductive organs. It would appear that the development of strains resistant to a specific disease will not necessarily solve the problem of establishing viable strains of laying stocks.

Lambert (1935) has pointed out the desirability of developing a long time program involving the intercrossing of relatively resistant strains, once they are established, and inbreeding the more resistant strains which can later be used for topcrossing and as foundation stock for intercrosses. Carpenter and Martin (1939) have suggested that relatively large populations of viable strains should be exposed in succession to a variety of diseases with the idea of determining whether the viability of the parental stock was due to lack of exposure and to determine which of the families of a strain possess resistance to a high degree. It was further suggested that when resistant families had been identified they could be used as foundation stock for inbred strains of resistant birds.

That the segregation of specific genes for susceptibility or resistance to disease initiated by pathogens may be responsible for immunity, morbidity, or mortality within the exposed population has been observed by Gowen (1937). Likewise, the segregation of genes for pathogenicity may make a pathogen virulent, mildly invasive, or innocuous, and the animal, due to its inheritance, may become a mosaic of cells, some of which are normal and some abnormal, so that the morbidity and mortality increase directly with the proportion of defective cells in the mosaic.

The inheritance of resistance to disease and the problem of breeding for viability is beset with many difficulties, as Jull (1936) has pointed out. Some of the difficulties include the following:

1. There is frequently considerable difficulty in determining the specific cause of death.

2. It is sometimes difficult to find strains or families having any resistance to a specific disease.

3. One of the greatest difficulties is the establishment of definite criteria of resistance.

4. Variation in bacterial virulence is a vital problem that sometimes occurs.

5. The difficulty of controlling the pathogenic organism involved in any study represents a problem of major importance.

6. The difficulty in distinguishing natural from acquired immunity interferes with the selective process.

7. Since resistance to infections is usually specific, there must be selection for each of numerous diseases, thus limiting greatly what can be accomplished in a general way, as Cole (1930, 1932) has pointed out.

8. Cole has also pointed out that selection for resistance to disease adds to the characters already being selected for, thus complicating the breeding program.

9. Genetic resistance is usually complex, being conditioned by multiple genes, the degree of interaction of which practically nothing is known.

10. It seems unlikely that all the genes conditioning resistance are cumulative in their action so that some of the genes in certain combinations lead to an increase in resistance but in other combinations lead to a decrease in resistance, the net effects depending upon the combination of genes associated with those that have been determined to be conditioners of resistance.

11. In order to secure the greatest degree of resistance in any strain of fowls, inbreeding combined with continuous selection would be necessary to bring about much increase in homozygosity beyond that accomplished by the first few years of selection.

12. A difficulty of paramount practical importance to the breeder would be that resistance once having been attained would require constant selection for its retention.

13. Granted that it might be possible to develop a strain of fowls highly resistant to a specific disease, there is always the possibility that mortality from other diseases may vitiate the results.

As far as the practical poultry breeder is concerned, he is advised to select breeding stock rigidly on the basis of the viability of their progeny from the time they are hatched to the time they are to be saved as breeders. Jull (1936) also suggested breeding only from yearling or older hens and never to use as breeders any birds belonging to families or strains in which there has been an appreciable incidence of mortality from any cause. Sires and dams whose progeny show a high incidence of mortality due to disease should be discarded and their progeny should also be discarded.

BREEDING FOR MEAT PRODUCTION

Chicken meat is sold in the form of broilers, fryers, roasters, capons, and fowl, the order of these classes of market chickens being arranged according to the age at which they are marketed. Within each class, there is usually considerable variability in body shape and degree of fleshing when the birds are dressed for market. Broilers, or roasters, or any other class of market poultry belonging to the same breed often exhibit variability with respect to body shape and degree of fleshing. In fact, judging by the appearance of dressed poultry usually offered to consumers, it is apparent that very little has been accomplished from the standpoint of breeding for uniformity of market type.

Likewise, very little seems to have been accomplished in the development of strains of chickens that will utilize feed most efficiently. It has been learned from practical experience in commercial broiler production that some strains of chickens require an average of 13 pounds of feed to produce a broiler weighing 3 pounds, whereas other strains require an average of only 10 pounds of feed to produce a 3-pound broiler. In producing roasters, there may be a difference between strains of as much as 6 pounds of feed required to produce a 6-pound bird. Since rate of growth is inherited, and since under ordinary circumstances body weight attained during any specific portion of the growing period is determined largely by the amount of feed consumed, it should be possible, by selection and breeding, to develop strains noted for their efficiency in the utilization of feed.

Poffenberger and DeVault (1937), in their analysis of commercial broiler production problems in Maryland, observed that, on the average, better results were secured from crossbred broilers than from purebred broilers because of the following factors: less mortality, slightly faster growth as indicated by somewhat heavier weight at selling time at 12.6 weeks of age for cross breeds, as compared with 13.7 weeks of age at selling time for pure breeds, less feed per pound of gain, and a little higher selling price per pound.

In the commercial production of broilers in Maryland, the most popular cross is Barred Plymouth Rock males mated to New Hampshire females and, in some cases, Rhode Island Red females. The particular reason for this cross being used is that more than one-half of the broilers produced are shipped alive to New York City where the Jewish people who require that the birds be killed under the

FIG. 69. A typical group of Barred Plymouth Rock males bred for slow growth. Average weight 17 ounces at 8 weeks of age. (Schnetzler.)

supervision of a rabbi prefer broilers with barred feathers. There is considerable demand, therefore, on the part of the hatchery operators who supply chicks to broiler producers for strains of rapid growing, early feathering Barred Plymouth Rock males and New Hampshire or Rhode Island Red females. Much more breeding work is necessary, however, to develop in sufficient quantity, the kind of breeding stock desired.

FIG. 70. A typical group of Barred Plymouth Rock males bred for rapid growth. Average weight 25 ounces at 8 weeks of age. (Schnetzler.)

Elsewhere in this country, other crosses are often made, such as White Wyandotte × White Plymouth Rock, Rhode Island Red × White Plymouth Rock, White Wyandotte × Barred Plymouth Rock, and White Plymouth Rock × Light Brahma. The results secured from any of these crosses depends largely upon the quality of the parental stocks that are crossed. Each parental breed should possess the inherent capacity for rapid growth and should also possess the factor for rapid feathering. For the most part, crosses between Leghorns

or other Mediterranean breeds and American breeds do not produce as satisfactory results as crosses among American breeds. Some results have been secured which indicate that satisfactory broilers may be produced by crossing White Wyandotte males with large-sized White Leghorn females. Where broilers are dressed at the producer's plant or where the market shows no preference for live broilers with barred plumage, the sex-linked barring factor need not be resorted to in making the crosses.

It must be emphasized, however, that although crossbreeding usually effects a stimulation during the early growing period, little benefit is to be gained by crossing purebred birds of poor quality. Many flock owners and hatchery operators who have purchased crossbred chicks have secured unsatisfactory results in growth and feathering because the purebred parents had not been bred to any extent for these desirable characteristics.

In Table 58 are given the average body weights in grams of purebred and crossbred chicks secured from various kinds of matings, numbers 1, 2, and 4 having been carried on for four years, numbers 3 and 5 for three years, and numbers 6 and 7 for two years. The birds were grown under range conditions.

TABLE 58. AVERAGE WEIGHT IN GRAMS, AT TEN WEEKS OF AGE, OF PUREBRED AND CROSSBRED CHICKS

(Knox, 1940)

Kind of Mating	Males	Females
1. Rhode Island Red ♂ × Rhode Island Red ♀	686	602
2. Light Sussex ♂ × Light Sussex ♀ ♀	681	602
3. White Wyandotte ♂ × White Wyandotte ♀ ♀	684	600
4. Rhode Island Red ♂ × Light Sussex ♀ ♀	720	646
5. Rhode Island Red ♂ × White Wyandotte ♀ ♀	702	618
6. L. Sussex ♂ × F_1 ♀ ♀ from R. I. Red ♂ × W. Wyandotte ♀ ♀	639	551
7. W. Wyandotte ♂ × F_1 ♀ ♀ from R. I. Red ♂ × L. Sussex ♀ ♀	694	596

The crossbred male and female chicks secured from the matings of Rhode Island Red male × Light Sussex females and Rhode Island Red male × White Wyandotte females were heavier at ten weeks of age than the purebred chicks of the same sex. The three-way cross of the male of one breed mated to the F_1 pullets secured from a cross of the other two breeds apparently had no beneficial effect, the males and females of these three-way crosses actually weighing less in some cases than purebred chicks of the same sex.

Lloyd (1939*a*, 1939*b*) has shown that in the case of Barred Plymouth Rocks, and Rhode Island Reds, it is possible to combine efficiency of egg and meat production in the same strain. Each breed averaged over 200 eggs during their first laying year for several years and the cockerels produced each year, were graded into grades A, B, and C. It was observed that, by the selection of the breeding stock over a period of years, 70 per cent of the birds attained the A grade and the number of slow-feathering males was reduced from 6 to 3 per cent in Barred Plymouth Rocks and from 30 to 10 per cent in Rhode Island Reds. It was also found that in some families, the males feathered out as early as the females.

Efficiency in the production of roaster meat is influenced by the rate of growth attained throughout the growing season, by the type of body, and by the fleshing ability. Maw and Maw (1938) have shown that body type in the sire has a definite influence on the body type of the male progeny, and Maw (1939) has observed that in strains within a breed there is often great variability with respect to body size and type. He has pointed out that the principal aim of the poultry breeder should be to control the body type of the progeny by selecting breeding stock on the basis of skeletal proportions which enable the bird to produce an abundance of flesh.

Jaap and Penquite (1938) have observed that the most desirable measure of body shape in live birds is the relation between the cube root of the body weight and the length of the shank. Jaap (1938) has shown that shank length serves as a good index of skeletal size and that in females shank length remains constant after five months and in males after six months. It is possible, therefore, to select females and males, respectively, at these ages, that will develop into the size of bird required at maturity. For a given shank length at five months of age in females and six months of age in males, the heaviest birds will be the heaviest birds at maturity. Also, given two roasters having the same shank length at seven months of age, the heavier bird should make a superior market carcass.

Jaap (1938) has also pointed out that among birds bred according to the Standard of Perfection shank length divided by the cube root of weight is in a ratio of 50 for Wyandottes and Orpingtons, 52 for Plymouth Rocks and Rhode Island Reds, and 54 for Leghorns. Shank length in males is 25 per cent greater than shank length in females, and body weight in males is 35 per cent greater than body weight in females of approximately the same age.

Annin and Halpin (1938) found no material difference in the rate of growth or in body weight at 28 weeks of age between cockerels and

capons, whether purebred or crossbred. Landauer (1937) found that the castration of Creeper and other male chicks at hatching time did not produce any changes in the absolute or relative length of the bones of the extremities to ten months of age, this observation being in conformity with that of Mansi and Hashimoto (1927).

Maw and Maw (1935, 1939) observed a definite relationship between body measurements and gains made in fleshing during the fattening process and the percentage of flesh of the whole carcass. According to Maw (1939), relatively greater gains in fleshing were made by birds that had relatively the greatest depth of body.

Broilers and roasters usually differ with respect to the percentage of edible flesh to the live body weight and dressed weight as shown in Table 59.

TABLE 59. PERCENTAGE OF EDIBLE FLESH IN BROILERS 10 WEEKS OF AGE AND ROASTERS 30 WEEKS OF AGE

(Maw, 1933)

Breed and Class	Waste as Percentage of Live Weight	Waste as Percentage of Chilled Dressed Weight	Percentage of Bone in Chilled Dressed Weight	Edible Flesh		Total Edible Flesh and Giblets	
				Percentage of Live Weight	Percentage of Chilled Dressed Weight	Percentage of Live Weight	Percentage of Chilled Dressed Weight
White Leghorn broilers:							
Males	33.83	24.62	25.78	37.14	43.30	42.62	49.69
Females	32.69	22.76	25.66	37.84	44.22	43.61	50.95
Barred Plymouth Rock broilers:							
Males	29.71	22.21	27.13	38.47	43.98	43.77	50.04
Females	30.63	21.86	25.33	39.60	45.46	45.19	51.88
Rhode Island Red broilers:							
Males	30.40	21.80	27.93	39.01	44.87	43.90	50.49
Females	30.98	22.05	27.37	38.18	43.82	44.10	50.60
White Wyandotte broilers:							
Males	29.38	22.31	27.06	39.60	44.73	45.82	51.76
Females	29.86	22.87	23.88	41.59	47.16	47.71	54.11
White Leghorn roasters	29.01	19.68	22.17	43.39	52.76	48.23	58.64
Barred Plymouth Rock roasters	24.81	16.92	22.18	47.99	55.12	51.84	59.33
Rhode Island Red roasters	24.68	16.98	20.72	49.08	57.09	52.79	61.40
Buff Orpington roasters	24.37	16.15	19.44	50.62	58.06	54.30	62.29

Greater uniformity of body type and better fleshing ability could probably be attained in almost any flock by a more rigid selection of

the breeding stock. Good depth of body in relation to shank length and reasonably good length of keel are desirable characteristics in breeding stock used for the production of broilers and roasters. In addition, the breeders should be able to transmit rapid growth and early feathering to their progeny. By selecting breeding stock from among families, the members of which exhibit these characteristics to a high degree, much could be accomplished in developing strains noted for efficiency of flesh production.

According to Brown (1938), the Canadian Government has adopted a policy of judging live and dressed poultry exhibited at fairs on the basis of prizes awarded for the best families of birds that meet certain qualifications. This is a most commendable procedure because it encourages poultrymen to think in terms of the relative quality of the progeny produced by different matings.

BREEDING FOR EGG PRODUCTION

The principal objective in breeding for high egg production is to increase the efficiency of the laying stock in the utilization of feed, since the feed consumed by layers constitutes about one-half of the total costs involved in egg production.

The amount of feed consumed by laying pullets during the first year of egg production has been determined at several institutions, the more important factors affecting the amount consumed being the kind of diet, the size of the birds, and the number of eggs laid. From data obtained at a number of state experiment stations, it is found that Leghorns laying an average of approximately 150 eggs per bird consume about 70 to 85 pounds of feed per year and that Plymouth Rocks and other breeds of similar size with an average egg production of 150 eggs consume about 80 to 95 pounds per year. The relationship between egg production and feed consumption is borne out by the data in Table 60, which gives the average number of pounds of feed required to produce one dozen eggs by groups of White Leghorns differing in average egg production per bird.

The data in this table show that the higher the egg production the greater the feed consumption per bird but the fewer the number of pounds of feed required to produce a dozen eggs. The poor layers used relatively more of the feed that they consumed for maintenance of body weight than the good producers.

The four outstanding characteristics of a good layer include earliness of sexual maturity, good rate of laying, nonbroodiness, and persistence of production. These four characteristics must be developed in a flock in order to provide for most efficient egg production

TABLE 60. POUNDS OF FEED CONSUMED PER DOZEN EGGS PRODUCED, ACCORDING TO AVERAGE EGG PRODUCTION PER BIRD, IN WHITE LEGHORNS

(Waite, 1934)

Average Egg Production per Bird	Average No. Pounds Feed Consumed per Bird	Average No. Pounds Feed per Dozen Eggs
117.7	69.30	7.06
136.6	71.41	6.28
145.0	73.25	6.06
156.3	75.32	5.78
165.8	76.67	5.55
175.0	77.82	5.34
185.0	78.64	5.10
194.4	80.99	5.00
204.8	81.02	4.75
214.8	81.84	4.57
224.6	83.48	4.46
234.1	84.28	4.32
243.9	85.36	4.20
253.9	87.03	4.11
269.2	83.73	3.73

By sexual maturity is meant the age of a bird in days at the time she commences laying. In order to lay 200 or more eggs during her first laying year, a White Leghorn pullet should commence laying at approximately 170 to 180 days, and members of the general-purpose breeds, at approximately 190 to 200 days. Precocious sexual maturity is to be avoided because such birds are apt to be quite small and will lay very small eggs for some time after laying has commenced.

Rate of laying is computed by determining on a percentage basis the number of eggs laid during a given number of days during which no serious pauses because of broodiness, or because of other reasons, have occurred. Rate of production is a more practical measure of determining rate for the poultryman and is determined by figuring, on a percentage basis, the number of eggs laid from the date of the first egg to a given date in relation to the total number of days involved. On this basis of determining rate, pullets of all breeds should lay at a rate of about 60 per cent in order to lay 200 or more eggs during the first laying year.

Broodiness is easily identified by virtue of the fact that the "clucker" remains on the nest overnight. From the practical stand-

point, the broody hen should be "broken up" immediately by placing her in a wire-floored or slat-bottomed coop, where she should be fed and watered regularly in order that she may be restored to laying condition as soon as possible. The economic importance of reducing broodiness in a flock is shown by the difference in egg production between Rhode Island Reds that went broody and those that showed no broodiness in highly bred flocks kept at the National Agricultural Research Center. The birds that went broody once or more during the year averaged 180 eggs, while those that did not go broody averaged 205 eggs. At the same institution, it was shown that the average production of nonbroody White Leghorns was 194 eggs compared with 153 eggs for those that went broody. Broodiness among Leghorns is usually not a serious problem but among the general-purpose breeds may be a very serious problem if it is not eliminated by a simple method outlined shortly hereafter.

Persistence of production simply means that during her first laying year, a bird continues laying well toward the end of her laying year, which is usually regarded as 365 days from the date of the first egg. The date on which the last egg is laid is probably the best measure of persistence, but from a practical standpoint the number of eggs laid during August and September of the year following that in which the bird was hatched is a more simple method of identifying the persistent producers. Birds that lay 25 or more eggs during August and September should have laid approximately 200 eggs or more at the close of their first laying year.

Body Weight and Egg Production. The relationship between body weight and egg production has been studied by a few investigators, from whose observations it is possible to draw only tentative conclusions. In general, it would seem that in a flock that has not been bred especially for high egg production, there is a tendency for the largest birds to lay relatively the fewest eggs. On the other hand, in flocks that have been bred for high egg production and where selection for body size has been practiced in the breeding program there appears to be little correlation between body size and egg production. The problem of maintaining good body size is important, however, inasmuch as it has been shown in Chapter VIII that egg size is rather definitely correlated with body size.

Platt (1927) suggested that White Leghorns should attain a body weight of approximately 4 pounds before the winter of their first laying year and that this weight should be maintained or slightly increased throughout the life of the birds. Robertson (1931) submitted evidence indicating that, among birds of various breeds entered in

Canadian egg-laying contests, there was a tendency for the larger sized birds to lay better than the smaller sized birds, but Sherwood (1922), Hervey and Lewis (1924), Jull (1924), and Platt (1927) submitted data showing little or no correlation between body weight and first-year egg production. Knox (1934) showed that in certain flocks there was a negative correlation between body size and egg production. Hays (1939) found that mature body size in Rhode Island Reds showed a significant negative correlation with annual egg production, but it was also indicated that pullets which increased 1 pound in weight during the first laying year gave the most satisfactory egg records.

In view of the observations of Asmundson (1921), Sherwood (1922), Hall (1923), Platt (1927), Waters (1927), Hervey and Lewis (1924), Jull (1924), Sherwood and Godbey (1928), Atwood and Clark (1930), Jull, Quinn, and Godfrey (1933), and Hays (1939), it may be said that there is a general tendency for large-sized birds to lay less well than small-sized birds but that it is possible to combine good body size and good egg production in the same flock.

Body Shape and Egg Production. The observations made by several investigators on the relationship between body shape and egg production are in agreement, for the most part, in showing that at times entirely too much emphasis has been attached to body shape as an index of egg laying ability.

The observations of Asmundson (1921), Hall (1923), Knox (1924), Knox and Bittenbender (1927), and Rice, Hall, and Marble (1930) indicate that certain body measurements are correlated with egg production. On the other hand, the observations of Sherwood (1922), Scholten (1927), Sherwood and Godbey (1928), van Rooyen (1932), Jull, Quinn, and Godfrey (1933), and Miller and Carver (1934) indicate that body measurements cannot be used as an index of egg-producing ability. Scholten (1927) pointed out that, although some of the correlations he obtained were significant, they were not sufficiently high to be of practical value in selecting birds.

Jull, Quinn, and Godfrey (1933) divided a flock of 237 White Leghorns that had completed their first year of egg production into three groups comprising highest, intermediate, and lowest producers, the average egg production of each of which was 245, 200, and 156 eggs, respectively. Measurements were made of the length of the back and keel and of the width of the back on the live birds and then on the dressed carcasses. The differences in live-bird and dressed-carcass measurements among the three groups of producers were found to be practically negligible. The differences between the length and width

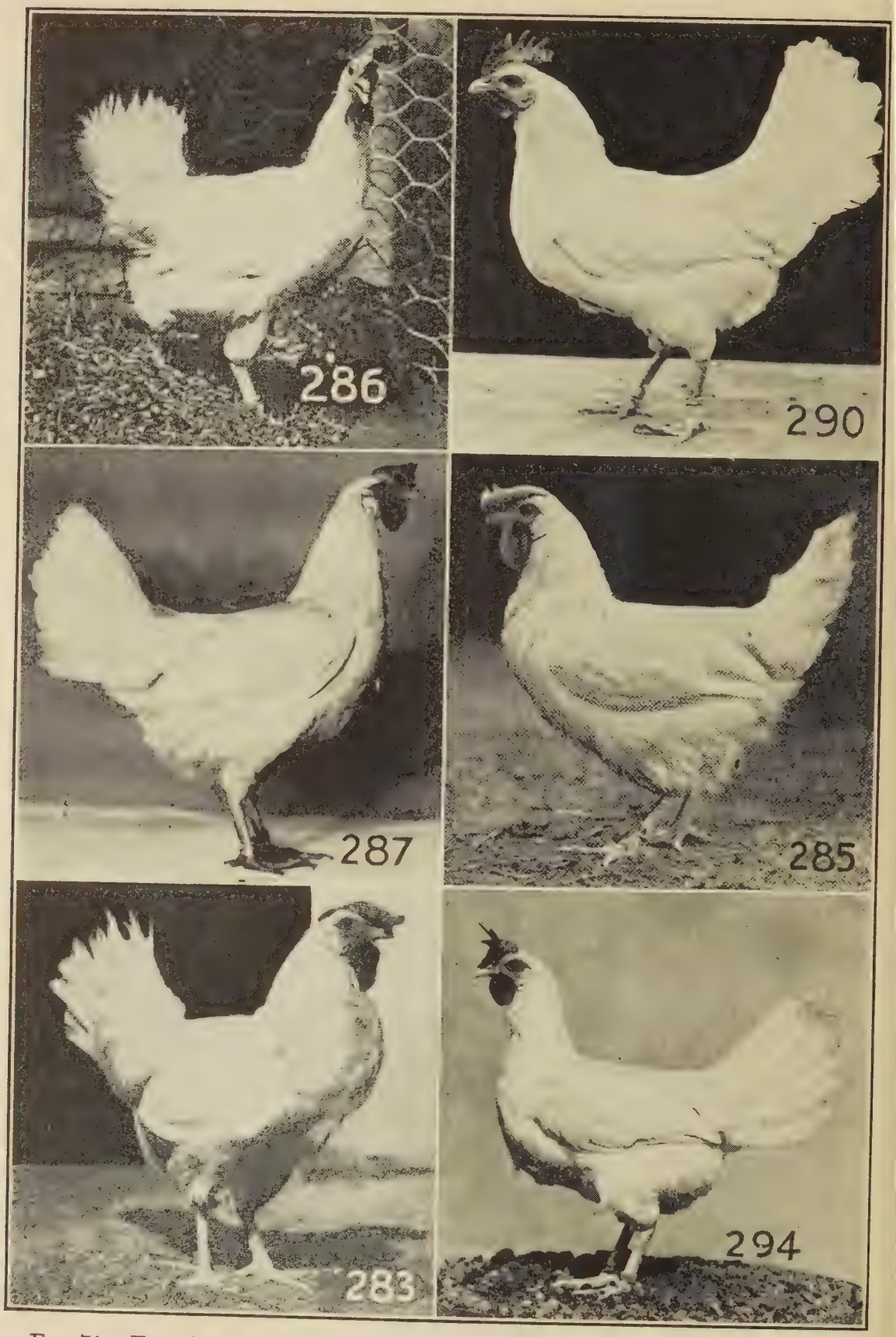


FIG. 71. Females of the same variety may vary considerably in outward appearances but still lay approximately the same number of eggs. The laying ability of a bird is determined by its breeding.

of the backbone and the length of the keel bone between the highest and lowest producers were so slight that these three characters could not serve as an index of laying type.

It has been shown by Knox and Bittenbender (1927) that measurements taken at intervals of a few weeks sometimes give significantly different results. It is known that changes sometimes take place with respect to the amount of fleshing over the bones during the first laying year, but it is also known from the observations of Schneider and Dunn (1924) that after pullets commence laying the long bones of the body change very little with respect to their relative lengths. It seems quite certain that as far as skeletal dimensions are concerned, body shape is not related to egg production.

Head Type and Egg Production. For several years, the importance of type of head in relation to egg-laying ability has been stressed by a number of workers. Waters (1927) studied the relationship between head type and egg production in 200 White Leghorns that had completed their first laying year in a Storrs Egg Laying Contest and found a slight positive correlation between depth of head and egg production and a slight negative correlation between width of head and egg production. Fronda and Gamo (1931) compared different head measurements with egg production in 75 Cantonese pullets and 111 Cantonese hens and reported positive correlations between egg production and the width and the depth of the beak but negative correlations between egg production and the distance from the base of the comb to the top of the eye and the distance from the top of the eye to the nostril.

Marble (1932) used six length, two depth, and six width measurements on the skulls of 100 White Leghorns and 47 Barred Plymouth Rocks and concluded that the shape of the skull bears no relationship to egg-laying ability. Measurements of the length, depth, and width of the skulls of 51 White Leghorns led Jull, Quinn, and Godfrey (1933) to conclude that not in a single instance was there any significant correlation between any of the measurements and egg production.

Jull, Quinn, and Godfrey also found live-bird head measurements made on 52 White Leghorns and 50 Rhode Island Reds were not indicative of egg-producing ability. Among 319 White Leghorns and 113 Rhode Island Reds, Miller and Carver (1934) observed that live-bird head measurements do not indicate productive capacity, nine different measurements having been made. Clevenger and Hall (1935) made 15 live-bird head measurements on 262 White Leghorns and found that there was no linear correlation between head measurements and egg production. On the other hand, it was found that the correla-

tion between head measurements and egg production was curvilinear, from which it was concluded that birds could be sorted into four different groups on the basis of head characters. It should be observed, however, that the difference in average egg production between certain pairs of the four groups was not significant.

Physical Appearance and Production. There are certain physical characters the appearance of which indicates whether or not a bird is in laying condition. If the comb and wattles are fully developed, bright red, and waxy in appearance, the bird is probably laying heavily; but if they are cold, dried, and shrunken, the bird is not laying. The small, round vent of the pullet becomes enlarged, oval in shape and moist when the bird is in active laying condition. Hammond and Burrows (1937) have shown that neither the size nor type of the female genital eminence is related to laying ability. The pubic bones, two small bones at the sides of the vent, become spread apart when the bird is in laying condition, and continuous production causes them to become thin and pliable. The abdomen, which contains most of the digestive and reproductive organs, should be of good size, and the skin covering the abdomen should be soft and pliable, in contrast to the thick and coarse skin often observed in poor layers.

Although neither the shape of the head nor the shape of the body is a reliable indication of laying ability, birds with extremely narrow or very coarse and "beefy" types of heads and bodies are usually poor layers.

Physiological Changes and Egg Production. Careful observation has shown that certain physiological changes take place in the body of the bird as egg production continues. The two physiological changes of greatest importance that are useful in determining persistent layers are the bleaching of the yellow pigment in the skin of yellow-skinned breeds and the time and duration of the first annual molt.

In all American and other yellow-skinned breeds there is usually an abundance of yellow pigment in the beak, shanks, toes, vent, and eyering and in the white of the earlobe of breeds having normally white earlobes. When a pullet starts to lay, the yellow pigment of the feed, called "xanthophyll," is diverted to the yolks of the eggs instead of going to the beaks, shanks, and other parts noted previously. As long as egg production continues, these parts gradually lose their pigment so that they become bleached in appearance. It follows, therefore, that the longer a bird continues to lay the greater the degree of bleaching. The yellow pigment does not return to the beak, shanks, and other parts until production ceases.

Yellow corn and green feed contain xanthophyll; but, if white corn

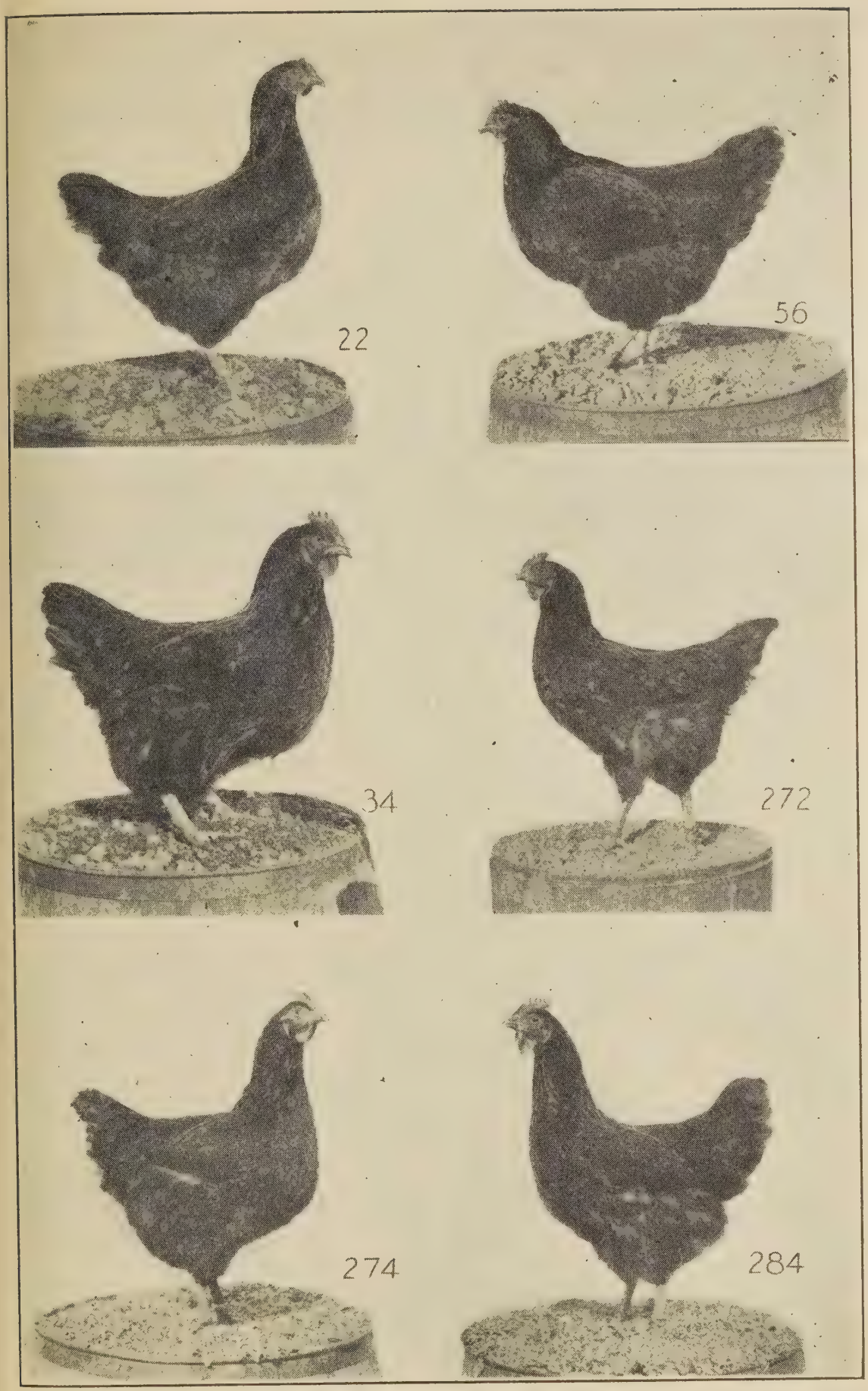


FIG. 72. In this group of Rhode Island Reds first-year egg production varied from 22 to 284 eggs. It would be difficult, except for differences in breeding, to tell why the bird in the upper left (22 eggs) and the bird in the center right (272 eggs) should differ by 250 eggs. The bird in the upper right (56 eggs) appears to lack vigor. The bird in the center left (34 eggs) inherited the tendency to produce flesh rather than eggs. The two lower birds are of superior breeding. (Photo by U. S. D. A.)

and other feeds that do not contain this yellow carotinoid pigment are fed, the beaks and shanks may be relatively pale even though the birds may have laid but few eggs. Therefore, the selection of persistent layers on the basis of changes in pigmentation should always take into account the kind of feed given the laying stock.

When yellow-skinned breeds are given feeds rich in xanthophyll, the extent of the bleaching of the vent, beak, and shanks serves as a very good indication of previous egg production.

TABLE 61. AVERAGE ANNUAL EGG PRODUCTION OF GROUPS OF WHITE LEGHORN HENS SELECTED ON THE BASIS OF VENT, BEAK, AND SHANK COLOR

(Data of Blakeslee, Harris, Warner, and Kirkpatrick, 1917)

Color Class	Number of Birds and Mean Annual Production					
	Vent		Beak		Shanks	
	Birds	Production	Birds	Production	Birds	Production
Pale	101	189.5	114	184.3	141	178.6
Medium	91	152.2	80	163.3	104	160.5
Yellow	183	136.3	181	131.8	130	123.4
Entire flock	375	154.5	375	154.5	375	154.5

The order in which the pigment disappears from different parts of the bird is first from the vent; then from the eyering, which is formed by the inner edges of the eyelid; then from the earlobes of breeds having normally white earlobes; then from the beak, beginning at the base and extending toward the tip; and finally from the shanks, disappearing first from the front of the shank and later from the rear. Under average conditions, a completely bleached beak indicates that the hen has been laying for four to six weeks, whereas completely bleached shanks indicate that the hen has been laying for fifteen to twenty weeks. When laying ceases, the pigment reappears in the different parts of the body in the same order in which it disappeared.

Under normal conditions, the average laying bird usually undergoes her first complete annual molt at the conclusion of what is known as her first year of laying. The time and duration of the first annual molt are important points in identifying the most persistent producers. Birds that molt early are usually the poorest layers, and, furthermore, the bird that is a poor layer usually stops laying in July and takes a

relatively long time to complete her molt. Extremely early molters are often out of production from four to six months and usually do not start their second laying year until December or January. Late molters, however, after a rest of two or three months, also begin to lay in December or January.

It usually takes about six weeks for a wing feather to grow out in either a low or a high producer, but the latter grows more feathers at a time, thereby completing the molt more quickly than a low producer. Some very high-producing hens take only a four- or five-week rest period. Exceptionally persistent producers sometimes have even shorter rest periods, production continuing during August, September, October, and November. Hens of this type usually begin to lay again before the new plumage is fully grown out. When the hen is molting, the feathers on different parts of the body are usually shed in the following order: head, neck, breast, body, wings, and tail. In some birds a few tail feathers may be shed before the wing feathers. Shortly after the old feathers are dropped, the new ones come in.

Early-hatched or early-maturing pullets sometimes have a partial molt in the fall of the year in which they were hatched, following a short period of production. The neck and tail feathers and one or two primaries (the stiff flight feathers seen on the outer part of the wing when it is spread out) may be shed during this molt; but the new primaries do not grow out to full length, and there is usually a break between the old and the new ones. During this molting period egg production usually stops, but, to avoid this period of nonproduction, many poultrymen try to keep their early-hatched pullets from going through a partial molt, although it is exceedingly difficult to check the partial molt; it may be avoided, however, by hatching at a later date.

When the selection of layers is made in August or September, toward the close of the first laying year, the condition of the plumage is good evidence as to whether or not the birds are persistent producers. The plumage of the persistent layers shows wear and tear from constant visits to the nest. The early-molting birds will have a growth of new feathers, the webs of which are glossy and bright in contrast to the dry, frayed webs of the old ones. The new quills are large, full, and soft, whereas the quills of the old feathers are small, hard, and almost transparent. A few pinfeathers in the neck may indicate a short molting period, but, when shedding extends to the body and wings, the molt usually becomes a complete one. A bird usually stops laying when molting the wing feathers but may lay while molting in other parts of the body. If the body weight is maintained, however,

exceptionally high-producing hens may continue laying until the wing molt is considerably advanced.

Ordinarily it is possible to estimate when the molt began by counting the primary feathers in the wing. The primary feathers are the stiff flight feathers seen on the outer part of the wing when it is spread out. The secondaries are also large and stiff, but they are found on the inner part of the wing and close to the body of the bird when the wing is folded in its natural position. The primaries are separated from the secondaries by a much shorter feather, known as the axial feather, which grows out at the wing joint.

There are usually ten primary feathers in each wing, and when the complete body molt begins the first primary to be dropped is the inner one next to the axial feather. In the case of the early molter, two weeks after the first primary is dropped the second one is shed, and at two-week intervals each subsequent primary is shed. In order to estimate the time elapsing since the molt began, six weeks should be allowed for the first mature new primary feather, and two weeks for each additional full-grown one. Thus a wing having four new full-grown primaries shows that the bird has been molting twelve weeks. If the molt has just begun and none of the primaries is yet fully grown out, calculation must be made on their present growth. Approximately two-thirds of this growth is made during the first three weeks, and the other third during the last three weeks. A half-grown primary, therefore, indicates about two weeks of growth.

Usually there is little difficulty in distinguishing the new primary feathers from the old ones because the new feathers are clean and bright with a soft quill and broad outline, whereas the old primaries are much more pointed in shape and are rather worn. The primaries of the persistent producer are molted rapidly and in a manner similar to that of the body plumage. Instead of being renewed one at a time, as in the early molter, a group of two or more primaries of the same length may grow simultaneously. When such a condition exists, all the new feathers of the same length are considered as one in calculating the length of time that has elapsed since molting began.

High-producing hens sometimes do not molt all their primary feathers but continue to carry some of the old ones into the next year. By growing the primaries in groups of two or more or by carrying over the old primaries, many high producers materially shorten the time necessary to complete their wing molt. It is apparent, therefore, that the time and duration of the molt serves as a good criterion of persistent production.

A carefully planned system of selection based upon the bleaching of

the pigment of the beaks, shanks, and other parts of the body and upon thorough observations on molting are extremely useful in segregating the high from the low producers in any flock.

Knox and Quinn (1936) made observations on 18 characters in their relation to egg production in 228 White Leghorns and concluded that most of these characters were correlated with each other, with the result that too much emphasis has often been given to the relationship between each of several individual characters and egg production. The character found to be most highly correlated with egg production was the bleaching of the yellow pigment in the shanks of the birds they studied.

Maintaining Efficient Flock Production. In order to maintain a high degree of efficiency in egg production in a flock, all sick birds and "loafers" should be removed regularly. Culling the flock at regular intervals serves the purpose of eliminating nonprofitable birds but also means that the birds that are retained will be among the most desirable ones to use for future breeding purposes. For the purpose of identifying nonlayers at any period during the first laying year, for the purpose of identifying the best layers up to a certain time, and for the purpose of selecting future breeders to develop a high-laying strain, the following chart submitted by Quinn (1934) should be consulted regularly.

For those who do not trap-nest their layers, the selection of females for future breeding purposes by their first-laying-year performance can be accomplished quite successfully. At the time each pullet commences laying, she should be banded with a numbered aluminum or colored celluloid leg band; a very simple way of determining the approximate time a pullet commences to lay is by noting the development of the comb and wattles and the width between the pubic bones. Pullets that lay at a high rate can be detected by the degree of the bleaching of the yellow pigment from the beak and shanks; during December or January, the layers should be examined and those which have the whitest beaks and shanks and are in good physical condition should be banded. Every time a bird goes broody she should be banded. Persistent layers could be identified by banding those birds that are laying well during August and September, just before the end of the year; note the condition of the comb and wattles (which should be red and expanded), the width apart and the flexibility of the pubic bones, the time of year of molting (note especially whether molting has taken place before September), and the well-bleached beak and shanks.

Such a system of banding is entirely practical and should do a great deal to enable the poultryman who is not trap-nesting to select

SELECTION CHART

(Quinn, 1934)

Characteristics Identifying Layers and Nonlayers

Character	Condition in a ———	
	Layer	Nonlayer
Comb	Large, bright, red, smooth, glossy	Dull, dry, shriveled, scaly.
Face	Bright red	Yellow tint.
Vent	Enlarged, smooth, moist	Shrunken, puckered, dry.
Pubic bones	Thin, pliable, spread apart	Blunt, rigid, close together.
Abdomen	Expanded, soft, pliable	Contracted, hard, fleshy.
Lateral processes	Prominent, pliable	Hard to find, stiff.
Skin	Soft, loose	Thick, underlaid with fat.

Characteristics Indicating Whether Previous Production Was Continuous or Brief

Character	Condition associated with ———	
	Continuous Laying	Brief Laying
Vent	Bluish white	Yellow tint or flesh color.
Eye ring and earlobe	White	Tinted with yellow.
Beak	White	Tinted with yellow.
Shanks	White, rather flattened	Yellow, round.
Plumage	Worn, soiled	Not much worn.
Molting	Late, rapid	Early, slow.

Characteristics of a High-Laying Strain

Time of maturity	Laying begins at about 6 months of age in the case of Leghorns and at about 7 months in the case of Rhode Island Reds, Plymouth Rocks, and similar breeds.
Rate of production	Average of 180 or more eggs a year.
Broodiness	Birds are seldom broody.
Persistence of production	Hens are laying well in August and September toward the end of the first laying year or after it is completed.

the best layers for breeding purposes. The banding of the birds should follow a definite method so that at the end of the year the best layers may be identified at a glance. If numbered aluminum bands are used, the numbers could be recorded under the four headings: earliness of maturity, rate of production, broodiness, and persistency of production. Numbers recorded under the first two and the last headings indicate desirable birds; numbers recorded under broodiness would indicate undesirable birds.

If colored celluloid bands are used, one color, such as red, should be placed on the left leg of each bird to denote earliness of maturity; another color, such as white, should be placed on the right leg of each bird to denote good rate of production; a black band should be used every time a hen goes broody; and a blue band should be used to identify the persistent layers. Red would thus signify an early start; white, bleaching after intensive laying; black, mourning for broodiness; and blue, persistency. At the end of the year, the best layers would each have a red, a white, and a blue band.

Disadvantages of Culling. A matter of great importance that tends to retard progress that might otherwise be achieved in the development of a high-laying strain is the fact that many pullets are culled before being allowed to complete their first-laying year. Disease and sickness are sufficiently good reasons for some of the culling, but other pullets are culled because they start laying late in life or lay at a slow rate or lay small eggs or for other reasons. Of course, a considerable amount of this culling is undoubtedly justified on purely economic grounds; the poultry breeder must make a living out of his business, and he feels justified in culling the birds that, he feels certain, have all the earmarks of uneconomical producers. At the same time, the practice of culling pullets during their first-laying year tends to destroy what is known as the random sample of a population.

What all progressive poultry breeders must sooner or later realize is that the best way of determining the relative merits of the sires and dams used each year is to keep a random or representative sample of their progeny. When only selected pullets are kept, it becomes impossible to tell whether the breeding birds from which they came were really capable of producing stock of high average merit. The pullets culled out as being too poor to keep may more nearly represent the breeding worth of their sires and dams than the pullets that were kept. This is a point that cannot be emphasized too strongly. A few prodigies of production are only "a drop in the bucket." It is the average production that must be constantly raised. From the standpoint of breeding operations, the practice of culling is in many respects

a negative procedure, whereas the practice of selecting the best birds for future breeding purposes is a positive procedure.

Selection on Basis of Egg Records. With a few outstanding exceptions, most of the poultry breeders in the United States apparently attach considerable significance to the first-year egg records of the females. There is a widespread belief that the higher the first-year record of the dam, the more eggs will her pullet progeny lay. In other words, it is claimed that the number of eggs a bird lays during her first laying year is a criterion of her breeding worth.

Data have been obtained from different sources which show that actually the first-year production record of a female is only of very limited value in predicting her breeding worth. A true test of the relationship that normally exists between the egg production of dams and the egg production of their daughters could be made only in the case of dams not selected on the basis of first-year egg-production records and complete families of daughters, *i.e.*, where no culling of pullets were practiced during the first laying year. Insofar as is known, however, no such data exist, for the simple reason that in practically all projects on breeding for increased egg production, the dams are selected to a greater or lesser extent on the basis of their first-year records.

However, data are available that show the relationship between the egg production of selected dams and the egg production of unselected daughters, the records of all daughters except those that died being included. In Table 62 are given data on Rhode Island Reds at the National Agricultural Research Center and on White Leghorns at the Mount Hope Farm. The Rhode Island Red dams were selected on the basis of having laid a minimum of 200 eggs their first laying year, whereas in the case of the White Leghorn dams the minimum given in Table 62 is 181 eggs.

The data on Table 62 show no apparent relationship between the egg production of the dams and that of the daughters among the Rhode Island Reds, but they show a slight relationship between the egg production of dams and that of the daughters among the White Leghorns.

It is interesting to observe that the average egg production of the daughters of each of the first six groups of the Rhode Island Red dams was considerably higher than the average egg production of the daughters of each of the comparable groups of the White Leghorn dams. The Rhode Island Red data were obtained from matings of yearling and older hens made in three consecutive years, 1928 to 1930, inclusive, the dams being mated to males whose dams laid 200 or more eggs during their first laying year. The White Leghorn data were

TABLE 62. THE AVERAGE FIRST-YEAR EGG PRODUCTION OF THE DAUGHTERS OF DAMS CLASSIFIED ACCORDING TO THE RANGE IN EGG PRODUCTION OF THE DAMS

Range in Egg Production of Dams	Average Egg Production of Daughters		Range in Egg Production of Dams	Average Egg Production of Daughters	
	Rhode Island Reds	White Leghorns[1]		Rhode Island Reds	White Leghorns[1]
181 to 190.....	—	162	251 to 260...	201	188
191 to 200.....	—	157	261 to 270...	200	209
201 to 210.....	188	168	271 to 280...	197	188
211 to 220.....	205	161	281 to 290...	179	208
221 to 230.....	192	173	291 to 300...	—	222
231 to 240.....	192	176	301 to 310...	—	228
241 to 250.....	199	169	311 to 320...	—	220

[1] Data from an unpublished paper by H. D. Goodale, 1935.

obtained from pullet matings made during the years 1923 to 1929, inclusive, and the low-producing dams listed in the table were used mainly during the first two or three years. Moreover, the sires used each year were selected on the basis of the records of egg production made by their sisters up to February first, from which it may be assumed that the males selected one year were somewhat superior to those selected the preceding year. The use of sister-tested males should in itself tend to increase the egg production of the daughters raised each succeeding year, even if the dams' records of egg production had been the same for each of the seven years.

Even so, it is apparent that the relationship between dam and daughter egg production is of a relatively low order. For instance, the group of White Leghorn dams with a range in production of 201 to 210 eggs had daughters that averaged 168 eggs, whereas the group of White Leghorn dams with a range in production of 271 to 280 eggs had daughters that differed by approximately 70 eggs, but their daughters' averages differed by only 20 eggs. The White Leghorn data show, however, that on the average the higher the egg production of the dams the higher the egg production of the daughters.

Those who hold that the egg-production record of a selected dam is an index of her breeding worth should examine carefully the source of the data on which their belief is based. In Table 62 it is shown that the White Leghorn dams that laid from 201 to 210 eggs had daughters that averaged 168 eggs each and that the dams that laid from 281 to

290 eggs had daughters that averaged 208 eggs each, the difference in the average egg production of the two groups of daughters being 40 eggs. On the other hand, the Rhode Island Red dams that laid from 211 to 220 eggs had daughters that averaged 205 eggs, whereas the White Leghorn dams that laid from 211 to 220 eggs had daughters that averaged 161 eggs, there being a difference of 44 eggs in the average production of daughters that came from dams with the same records. Then, again, those who claim that the first-year record of egg production of a bird is a good index of her breeding worth would have great difficulty in accounting for the fact that the Rhode Island Red dams with a range of 201 to 210 eggs and the White Leghorn dams with a range of 271 to 280 eggs produced daughters that had exactly the same average egg production.

Although the selection of dams on the basis of their first-year records of egg production is thoroughly justified, the data in Table 62 show that the production records by and of themselves are of very limited value. Some poultrymen have assumed, however, that, if it can be shown that in certain flocks there is a slight correlation between dam and daughter egg production, then it must follow that in all flocks the selection of breeding stock on the basis of individual records would rather quickly raise the level of egg production. These poultrymen usually overlook the conditions involved in selecting the breeding stock in those flocks where a dam-daughter correlation has been shown to exist, and they fail to realize that these conditions do not apply to the great majority of poultry-breeding flocks throughout the country. Most poultry breeders in the United States cull their pullet flocks rather closely, and many of them use individual records of egg production as the sole basis for selecting their breeding stock. While poultry breeders should be encouraged to select their breeding stock on the basis of production records, they should be cautioned not to attach too much significance to those records.

If the first-year egg-production records of a female served as an accurate index of her breeding worth, as some have claimed, the problem of breeding for increased egg production would be comparatively simple. The data in Table 63 show how divergent are the results sometimes secured from two groups of daughters produced by the same dam mated in different years to the same, or to different, sires. These data were obtained from the National Agricultural Research Center, the first five dams in the table being Rhode Island Reds and the second five White Leghorns. The daughters' averages given in the table were determined for all daughters produced by each mating except for birds that died.

TABLE 63. THE AVERAGE EGG PRODUCTION OF EACH GROUP OF DAUGHTERS OF DAMS MATED TO THE SAME AND TO DIFFERENT SIRES IN TWO DIFFERENT YEARS

Dam No.	Sire No.		Dam's Production	Average Egg Production of Daughters	
	1st year	2nd year		1st year	2nd year
Rhode Island Reds:					
6,024	176	176	212	217	189
6,027	176	176	206	178	222
6,401	334	334	233	214	184
5,829	325	338	246	189	241
6,142	351	368	242	182	220
White Leghorns:					
2,786	50	249	257	159	228
3,472	100	248	235	212	172
3,728	91	248	258	213	167
3,845	91	248	262	175	202
3,287	100	249	230	164	225

The data in Table 63 show that the same dam when mated to the same sire may produce daughters in two different years that differ in average egg production by as much as 40 eggs. When mated to different sires, the daughters of the same dam in successive years differ by as much as 60 eggs.

It is unfortunate for the poultry-breeding industry that many poultry breeders attach so much importance to individual records of production, especially since it has been shown that progress in breeding for increased egg production is bound to be achieved very slowly as long as a record of egg production is the only basis used in selecting the breeding stock.

Concerning the egg-production record of a dam, Pearl (1912) has stated that it "is not of itself a criterion of any value whatsoever from which to predict the probable egg production of her female progeny." Evidence in support of this statement has been submitted by Gowell (1903), Jull (1933), Petrov (1934), Munro (1937), and Taylor and Lerner (1938). It has also been shown by Jull (1934*a*) that the egg-production record of a sire's dam did not serve as an index of the breeding ability of the sire.

There are several reasons why the record of a bird's egg production may not be nearly so significant in indicating her breeding worth as many poultry breeders are inclined to believe. Egg production is a

quantitative characteristic which is easily influenced by environmental conditions and by the diet given the laying stock. Poorly balanced diets, improper methods of feeding, poor housing conditions, sudden changes in temperature, internal and external parasites, and diseases of various kinds all tend to decrease production. There may be a vast difference between the number of eggs a bird actually lays and the number she might have laid if she had been kept under ideal conditions. Rarely, however, do conditions prevail that would enable a bird to lay the number of eggs of which she is potentially capable.

Selection on Basis of Pedigree. By pedigree breeding in poultry is meant the mating of birds with pedigrees and the notation of the parentage of the chicks produced so that their pedigrees are a matter of record. A bird's ancestry sometimes gives considerable information of value regarding its probable worth as a breeder. Of two birds with the same first-year egg-production records, the one with a good ancestry is to be preferred to the one with a poor ancestry. The chances are greater that the former will give better results in breeding than the latter—the chances are greater, but there is no guarantee that a bird of good ancestry will always produce good progeny.

Although a good pedigree is of importance in selecting breeding stock, there are certain limitations in the application of pedigree selection. For instance, very little significance can be attached to the individual records of egg production of ancestors beyond the third generation. Then, again, the greater the variation in the environmental conditions—including diet, method of housing, and the use of artificial lights—to which a flock is subjected over a period of years, the less reliance can be placed upon the ancestors' records of production in the selection of progeny for future breeding purposes.

In Table 64 are given the average egg production records of the daughters of full-sister dams mated to the same sire in matings of White Leghorns and Rhode Island Reds. In the case of the White Leghorns, the dams used as breeders were selected on the basis of having laid a minimum of 225 eggs during their first laying year and the sires used were those whose dams had a minimum 225-first-year-egg-record. In the case of the Rhode Island Reds, the dams and the sire's dams were birds with a minimum 200-egg first-year record. It should be noted that no culling was practiced among the daughters during their first laying year.

The data in Table 64 show that when two or more full-sisters are mated to the same sire, the average egg-production records of the different groups of daughters may be on nearly the same level or may

TABLE 64. AVERAGE EGG PRODUCTION OF DAUGHTERS OF FULL-SISTERS MATED TO THE SAME SIRE

(Jull, 1933, 1934*a*)

White Leghorns				Rhode Island Reds			
Sire No.	Dam No.	No. of Daughters	Daughters' Average Egg Production	Sire No.	Dam No.	No. of Daughters	Daughters' Average Egg Production
3	3,428	8	239	173	5,829	8	209
	3,693	12	235		5,846	7	201
	3,769	5	245		5,928	5	207
249	3,287	5	242	338	6,502	7	188
	3,289	6	182		6,752	6	169
	3,695	8	207		6,792	6	204
250	4,086	4	242	363	6,537	9	211
	4,350	5	244		6,577	4	178
	4,451	5	220		6,750	7	221
3	3,767	6	219	330	6,200	10	208
	3,824	7	232		6,213	7	177
91	3,640	8	214	330	6,532	6	180
	3,845	5	175		6,668	8	207
250	3,289	11	189	352	6,264	6	169
	3,695	11	194		6,400	7	208

differ considerably. The full-sister dams represent a selected group and, although any two full-sister dams had different first-year egg records, it is doubtful if the difference was in any case significant. Full-sisters, of course, have identical pedigrees, so that the differences in the egg-production records of the daughters of full-sisters cannot be accounted for on the basis of pedigree.

Two interesting observations are worthy of mention in connection with the data in Table 64. In the first place may be mentioned the similarity of level of egg production among the groups of daughters of the full-sister dams mated to White Leghorn Sire No. 3 and Rhode Island Red Sire No. 173. In the second place may be mentioned the dissimilarity of level of egg production between the groups of daughters

of full-sister dams mated to White Leghorn Sire No. 91 and Rhode Island Red Sire No. 352.

Having shown that White Leghorn and Rhode Island Red dams each having a minimum record of 225 and 200 eggs, respectively, may

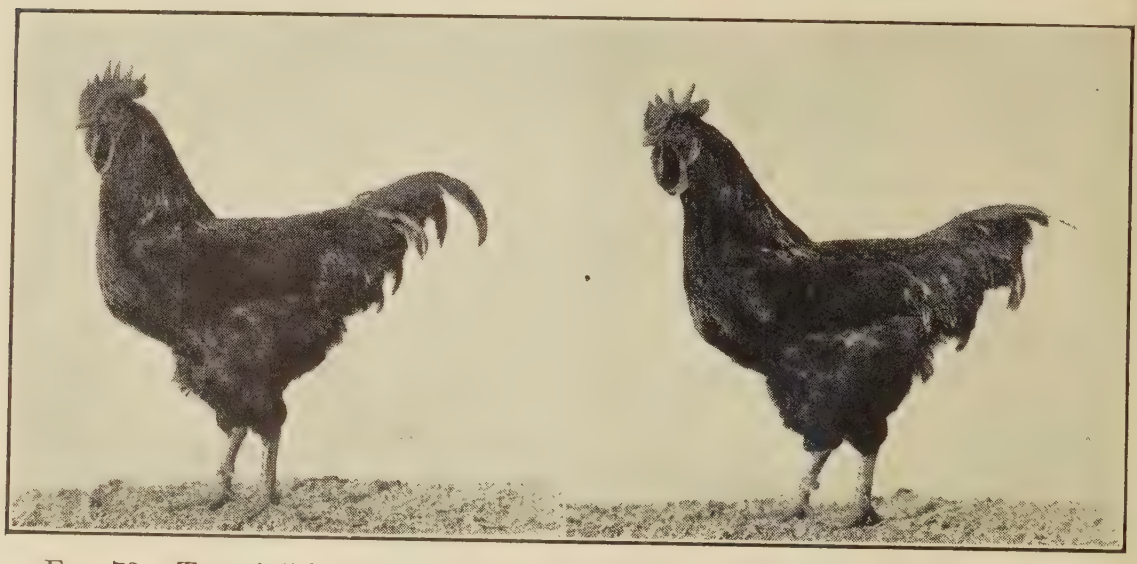


Fig. 73. Two full-brothers that gave distinctly different results in breeding. Their dam laid 229 eggs and their granddams 219 and 230 eggs each. Each male was mated to females that had laid 225 or more eggs in their first laying year. In the fall of the year the daughters of the two males were selected for the laying house on a family basis, each family having 5 or more full-sisters. Of the 17 selected daughters of the male on the left 4 died during the first laying year and the other 13 laid an average of 159.85 eggs each. Of the 39 selected daughters of the male on the right 3 died during the first laying year and the other 36 laid an average of 205.75 eggs each. The progeny test revealed the difference in the breeding value of these full-brothers, which, of course, had identical pedigrees. (U. S. D. A.)

produce progeny differing considerably in egg production, even when the dams are full-sisters, it is interesting to note that sires sometimes produce progeny differing considerably in levels of egg production even when they are full-brothers and are mated to dams of similar average

Table 65. Average Egg Production of Daughters of Full-Brother Sires Mated to Dams of Similar Potential Breeding Ability

(Jull, 1933)

Sire No.	No. of Dams	Dams' Average Egg Production	No. of Daughters	Daughters' Average Egg Production
200.....	6	243	52	193
10,105.....	9	242	49	216

potential breeding ability, as shown in Table 65, the breed being Rhode Island Reds.

The difference between the average egg production of the two groups of daughters is significant, showing that the two full-brothers differed in their breeding worth, although their pedigrees were identical.

The data in Table 66, pertaining to Rhode Island Reds and White Leghorns, show that the higher the egg production of the three nearest female ancestors of both sire and dam the higher is likely to be the average egg production of their progeny. In the case of each flock, the environmental conditions were kept as uniform as possible from year to year.

TABLE 66. THE AVERAGE EGG PRODUCTION OF DAUGHTERS ACCORDING TO THE RANGE IN AVERAGE EGG PRODUCTION OF THE THREE NEAREST FEMALE ANCESTORS OF BOTH SIRE AND DAM

Range in Average Egg Production of the Three Nearest Female Ancestors of Both Sire and Dam	Average Egg Production of Daughters		Range in Average Egg Production of the Three Nearest Female Ancestors of Both Sire and Dam	Average Egg Production of Daughters	
	Rhode Island Reds	White Leghorns[1]		Rhode Island Reds	White Leghorns[1]
209 to 217.....	186	—	254 to 262.....	—	199
218 to 226.....	197	180	263 to 271.....	—	213
227 to 235.....	199	166	272 to 280.....	—	216
236 to 244.....	205	176	281 to 289.....	—	222
245 to 253.....	—	208	290 to 298.....	—	210

[1] Data from an unpublished paper by H. D. Goodale, 1935.

Judging from the data in Table 66, it is apparent that the selection of breeding stock on the basis of ancestors' records of production to the third generation is of considerable importance. As a matter of fact, the more information there is in the pedigree concerning the records of egg production of the sisters of parents and grandparents, and the more information there is concerning the breeding performance of parents and grandparents and their relatives, the greater the value of the pedigree in selecting breeding stock.

A simple illustration from the Ontario Agricultural College may be given to emphasize the importance of complete records on a family basis in order to permit the wisest choice in selecting future breeders.

Two dams were mated to the same sire and each produced seven pullets the first-year egg production of each of which is listed under her dam

Family A Dam H46—262 Eggs Egg Production of Daughters	Family B Dam H12—258 Eggs Egg Production of Daughters
95	190
105	210
157	212
161	216
190	234
196	234
263	242

In Family A, the daughter that laid 263 eggs would in all probability prove to be a much poorer breeder than any of the daughters in Family B, including the one that laid only 190 eggs.

The relative importance of the average egg production record of families of full-sisters in relation to the average egg production of the daughters of one or more of the full-sisters is shown by the data submitted by Taylor and Lerner (1938).

Table 67. Average Egg Production of Daughters in Relation to Average Egg Production of Dams and Their Full-Sisters

(Taylor and Lerner, 1938)

Average Egg Production of Dams and Their Full-Sisters	Average Egg Production of Daughters
109	139
192	205
201	213
230	215

The data in Table 67 show that the selection of pullets and cockerels for future breeding purposes from families of full-sisters that have a relatively high average egg production would be well worth while. The family method of selecting breeding stock to build up a good laying strain is one phase of applying the progeny test in breeding for increased egg production.

Selection on Basis of Progeny Test. The supreme test of the worth of a bird as a breeder is the kind of progeny it produces. Thus

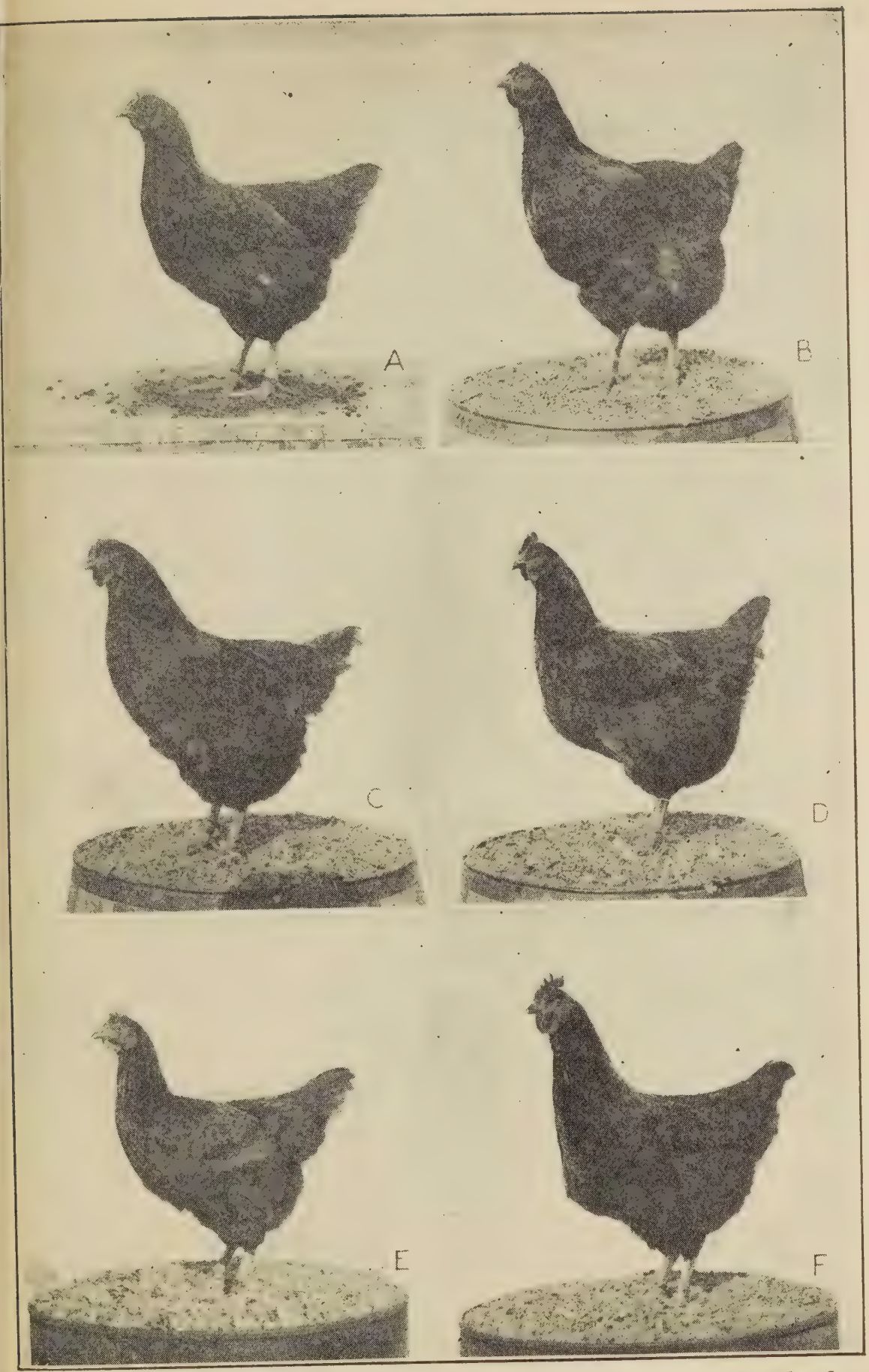


FIG. 74. A dam and five daughters. The dam, A, laid 236 eggs. The first-year records of the daughters are as follows: B, 208; C, 229; D, 232; E, 246; F, 259. (Photo by U. S. D. A.)

in the case of a dam it is not her individual laying record that counts so much as the average laying record of her daughters, which is quite a different thing. Strangely enough, the first impetus given to progeny testing in breeding for increased egg production was the failure resulting from an attempt to develop an egg-laying strain through the selection of female breeders based entirely on their first-year records of egg production. Apparently, the first attempt at a state institution to improve egg production through selection was made at the Maine Agricultural Experiment Station. The work was carried on many years ago with Barred Plymouth Rocks, and the records show that over a period of nine years the practice of selecting female breeders on the basis of their first-year trap-nest records failed to produce an increase in the level of egg production among the pullets raised each year.

The early work at the Maine Station, however, laid the foundation for later work which demonstrated the significance of the progeny test in breeding for increased egg production. Further breeding work with Barred Plymouth Rocks at the Maine Station demonstrated that by selecting each year cockerels and pullets for future breeding purposes from among the best families of that year a steady increase in the level of egg production was achieved. Cockerels and pullets to be used as breeders were selected from among the progeny of sires and dams that proved to be superior in breeding worth to other sires and dams. The progeny-test method of selecting breeding stock has been used consistently for a period of years in the breeding of Rhode Island Reds at the Massachusetts Agricultural Experiment Station, where outstanding results have been achieved.

The difference in breeding worth of sires mated to trap-nested Rhode Island Red dams having minimum first-year records of 200 eggs and White Leghorn dams having minimum first-year records of 225 eggs is shown in Table 68. The data were obtained from a few of the matings made at the National Agricultural Research Center. The records of egg production of all daughters placed in the laying houses, except for birds that died, were used to compute the average for each of the different groups of daughters. The mortality among Rhode Island Red daughters was 9.17, and among the White Leghorns 13.26 per cent. The average egg production of all the Rhode Island Red daughters was 192 and of all the White Leghorn daughters 193.

The data in Table 68 make it quite clear that certain sires were much superior to others from the standpoint of transmitting laying ability to their daughters. The sons and daughters of sires 173 and 3

TABLE 68. AVERAGE EGG PRODUCTION OF DAUGHTERS OF DIFFERENT RHODE ISLAND RED SIRES MATED TO RHODE ISLAND RED DAMS THAT LAID 200 OR MORE EGGS AND OF DIFFERENT WHITE LEGHORN SIRES MATED TO WHITE LEGHORN DAMS THAT LAID 225 OR MORE EGGS

Rhode Island Reds				White Leghorns			
Sire No.	Average Egg Production of Sire's Mates	Number of Daughters	Average Egg Production of Daughters	Sire No.	Average Egg Production of Sire's Mates	Number of Daughters	Average Egg Production of Daughters
173	223	48	219	3	248	45	229
10,105	242	49	216	250	243	37	227
334[1]	231	37	211	249	243	71	206
338[1]	238	31	206	252	247	48	200
334[1]	242	32	205	91	254	46	199
330[1]	246	46	201	100	248	59	193
330[1]	250	38	195	259	243	69	185
200	243	52	193	254	237	51	179
338[1]	250	60	192	10,106	239	46	179
351	232	75	171	50	228	49	168

[1] These sires were used in two consecutive breeding seasons.

are likely to be much better breeders than the sons and daughters of sires 351 and 50.

Some poultry breeders carry on progeny-testing work on an extensive scale and, from the various matings made, retain either all the progeny or a sufficiently large number to make it possible to concentrate breeding work among families that have been developed from superior sires and dams. The record made of a random sample of the progeny, of course, gives the most accurate index of the breeding worth of the breeder's flock or mating. The data in Table 69 were obtained from two private poultry breeders who practiced no culling of the progeny of different sires.

Poultry breeder *A* knows full well that sire G10, whose mates' average was 264 eggs and whose daughters' average was 219 eggs, is greatly superior in breeding worth to sire G11, whose mates' average was 285 eggs and whose daughters' average was 163 eggs. Likewise, *B*, with his White Leghorns, would pick Sire No. 1, whose mates and daughters averaged 283 and 243 eggs, respectively, over Sire No. 5, whose mates and daughters averaged 255 and 152, respectively. *B's*

TABLE 69. THE AVERAGE EGG PRODUCTION OF DAUGHTERS OF DIFFERENT SIRES USED IN TWO PRIVATE BREEDING FLOCKS

Poultry Breeder	Variety	Sire No.	Average Egg Production of Sire's Mates	No. of Daughters	Average Egg Production of Daughters
A	White Leghorns	G10	264	76	219
		G 8	276	84	218
		G 4	262	80	209
		G 7	261	135	198
		G 6	276	108	191
		G 2	274	105	166
		G11	285	114	163
B	White Leghorns	1	283	130	243
		2	289	39	240
		3	259	55	228
		4	273	18	169
		5	255	33	152
	Rhode Island Reds	1	252	57	242
		2	277	104	235
		3	268	26	234
		4	237	39	168
		5	270	28	165

Rhode Island Red Sire No. 1 was mated to females that averaged 252 eggs, and his daughters averaged 242 eggs; whereas Sire No. 5, although mated to females that averaged 270 eggs, had daughters that averaged only 165 eggs.

The relative importance of progeny testing in breeding for increased eggs production has been emphasized by Warren (1932), Knox (1933), Munro, Bird, and Hopkins (1937), Hopkins, Munro, and Bird (1937), Bird and Sinclair (1938), and Goodale (1938), who obtained an increase of 53 eggs per bird from 1923 to 1929, inclusive, by employing the family-method phase of progeny testing White Leghorns.

The breeding program should be based on the selection of outstanding families. Sires and dams that have proved to be of outstanding breeding worth should be used for as many years as possible. Also, their progeny should be given preference when the time comes to select future breeders. Since the average sire and dam are relatively short-lived creatures, however, it is necessary to adopt the best system

possible in the selection of younger birds for breeding purposes, especially cockerels. For this purpose, it is necessary to determine which family of full-sisters is giving the best performance during the fall and early winter from the standpoint of early sexual maturity and rate of laying, because the cockerels must be selected about the first of the year. Cockerels for future breeding purposes should be chosen from the families in which the full-sisters are outstanding.

The larger the number of progeny of each female and each male used as breeders, the greater is the degree of reliability in the selection of superior families. On the other hand, it should be noted that, while the average reliability increases with the number of offspring, it is proportional to the square root of the number of offspring, not to the absolute number of offspring. In other words, the average record of egg production of 16 daughters has *twice* the average reliability of the average record of egg production of 4 daughters.

It may be worth while to point out that to be able to identify a male of superior breeding worth is much more important than to be able to identify a female of superior breeding worth, for the simple reason that a sire has, on the average, several times as many progeny as a dam, depending upon the number of females to which the male is mated. At the same time, females of superior breeding worth are the only ones from which males of superior breeding worth can be obtained.

A criterion for determining the reliability of trap-nest records made under official supervision has been developed by Hendricks (1937).

Poultrymen who do not trap-nest their layers and do not carry on pedigree breeding work are able, however, to apply the progeny test to males. The plan suggested by Hagedoorn (1926) should prove to be valuable to many poultrymen. The males to be tested must be mated to a certain number of females, and the progeny of each male must be kept in a separate laying house. By comparing the average egg production of the progeny of each male, the poultryman should be able to determine which male to use again if desirable, and he should also be able to decide from which male's progeny to select cockerels and pullets for future breeding purposes.

The Connecticut record-of-performance breeders employ a method of determining a criterion of the breeding worth of a record-of-performance breeder's breeding stock which might be followed by others. The index used is called "hen-housed flock average" and is computed by dividing the total number of eggs laid during the year by the original number of pullets placed in the laying house at the beginning of the year. It is obvious that the flock suffering the

greatest mortality would be the one most severely handicapped, s that the hen-housed flock average serves the purpose of an index o relative viability as well as an index of relative breeding worth wit respect to egg production.

Selection on Basis of Egg Characters. In addition to character pertaining to egg production, those that should be taken into con sideration in the selection of birds for breeding purposes include siz of egg, shell color and thickness, and albumen quality.

In Chapter VIII egg weight has been shown to be influenced by a variety of factors, one of the most important of which is body size

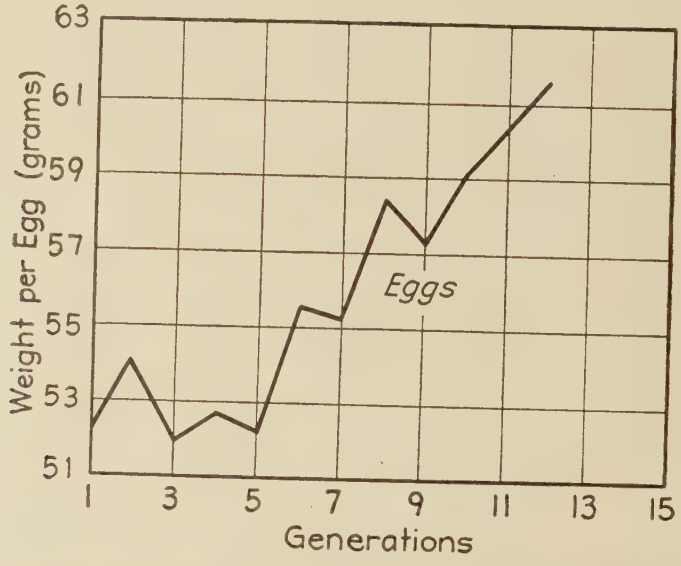


FIG. 75. Increase in egg weight in the Mount Hope flock under the family or progeny-test method of breeding. No efforts were made to increase egg weight until the sixth generation. (Goodale, 1938.)

In order that laying pullets may lay eggs approximating standard weight reasonably soon after laying commences, it would appear desirable to have the following weights attained at commencement of laying: Leghorns, at least 3 pounds and preferably 3.5 pounds; Rhode Island Reds, New Hampshires, and Wyandottes, at least 4.5 pounds and preferably 5 pounds; Plymouth Rocks at least 5 pounds and preferably 5.5 pounds. Undersized birds should be rejected. Eggs selected for hatching should approximate 2 ounces each. The progeny test should be applied both in selecting potential breeders for body size and in selecting for egg weight. It should be kept in mind by those whose flocks lay undersized eggs throughout the year that a permanent new level of increased egg weight is established only when further selection to maintain this level becomes unnecessary.

For poultry breeders who desire to take into consideration simultaneously the number and the weight of eggs in the selection of breeding

stock, the following scale of points for size of egg will be found convenient:

20 ounces per dozen	0.80
21 ounces per dozen	0.85
22 ounces per dozen	0.90
23 ounces per dozen	0.95
24 ounces per dozen	1.00
25 ounces per dozen	1.05
26 ounces per dozen and over	1.10

By the application of this scale of points it is apparent that a bird laying 210 eggs averaging 24 ounces per dozen would score 210 points; a bird laying 190 eggs averaging 26 ounces per dozen would score 209 points; a bird laying 260 eggs averaging 20 ounces per dozen would score 208 points.

In Leghorn and other "white-egg" breeds, it is highly important that all eggs produced be entirely free of tints. In flocks producing a considerable proportion of tinted eggs, the practice of eliminating tinted eggs from among those saved for hatching could not be expected to accomplish much for several years, because birds laying the tinted eggs would be left in the flock. On the other hand, several generations of selection for the purpose of eliminating not only the birds that lay tinted eggs but also the parents of such birds should result in reducing to a minimum the proportion of tinted eggs laid by a flock. As far as the production of brown-shelled eggs is concerned, it is doubtful if selection, except very rigid selection for several generations, would accomplish much in the direction of developing uniformity of any particular shade of brown.

Since thickness of egg shell is inherited, it should be possible by progeny testing to develop strains laying eggs with relatively thick shells, but for the average poultryman this would be rather difficult because of the details involved in measuring shell thickness. Relative differences in thickness of shell among eggs laid by different hens might be determined by incubation to ascertain loss in weight, but again this would be a rather laborious procedure for most poultrymen. From a practical standpoint, probably the best the average poultryman could be expected to undertake would be to eliminate birds laying eggs of poor shell texture and also reject from the breeding pens all ancestors of such birds.

The percentage of thick white to the total white of the egg has been shown to be an inherited characteristic, and it has also been shown that it is possible to develop by selection, strains that differ significantly with respect to this characteristic. Pedigree breeders

could probably accomplish something in the direction of developing strains noted for the high percentage of thick white to total white in the eggs laid by breaking out a certain number of eggs laid by each hen and then applying the progeny test in the selection of future breeders. From the standpoint of the average poultryman, however, it would

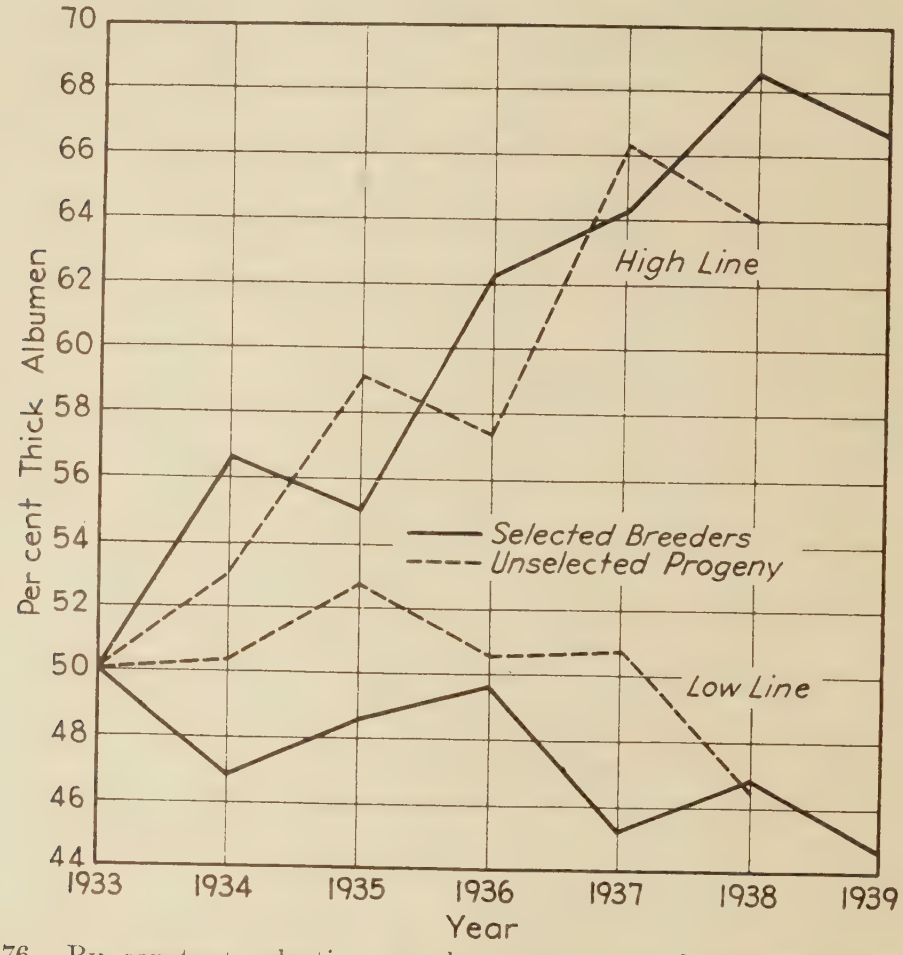


FIG. 76. By constant selection on the progeny-test basis two separate lines have been developed, one line laying eggs with about 65 per cent thick white of total white and the other line about 45 per cent thick white of total white. (Olsen and Knox, 1940.)

seem to be very desirable to have developed an improved egg-candling technique that would enable the poultryman to determine by candling methods those birds that lay eggs possessing a relatively high percentage of thick white to total white.

PROBLEMS

1. Discuss the relative importance of the following 6 points in the development of a flock for the purpose of providing the largest possible revenue from the sale of baby chicks, breeding stock, market poultry, and market eggs: (*a*) constitutional vigor, (*b*) plumage color, (*c*) freedom from standard disqualifications, (*d*) egg production, (*e*) size of eggs, (*f*) color of egg shell.

2. Which of the two following practices is the more logical one for a poultry breeder to follow: (*a*) breed first for high egg production, disregarding all other matters, then breed for egg size, then breed to eliminate any standard disqualifications that may be common in the strain, then breed for good head characters in the breeders, and finally breed for perfection in plumage coloration; (*b*) breed for perfection in all five characters simultaneously?

3. What is the most important point to be kept in mind if inbreeding is to be practiced?

4. In selecting male breeders tell how to select for (*a*) constitutional vigor, (*b*) good fertility and hatchability prior to the regular breeding season, (*c*) ability to produce good progeny.

5. From a flock of 375 birds that have just completed their first-year production, 75 are to be selected for future breeding purposes. Discuss the relative importance of the following 6 points in selecting the 75 best birds: (*a*) age at commencement of laying, (*b*) rate of egg production, (*c*) persistency of production, (*d*) size of egg laid during the first six months of laying, (*e*) size of bird, (*f*) the laying performance of each bird's full-sisters.

6. (*a*) What steps should hatchery operators take to insure good fertility in the flocks supplying eggs to their hatcheries? (*b*) A hatchery operator secures eggs from 15 different flocks, and, although all the flocks are given the same management, including the same kind of ration, and although the eggs from all the flocks are incubated under identical conditions, the hatchery operator finds that the eggs from 3 flocks hatch poorly and the eggs from 2 other flocks hatch very poorly. What should the hatchery operator do to improve the hatchability of the eggs from these 5 flocks?

7. Since egg production is relatively the most important branch of poultry production, outline a plan whereby commercial hatchery operators may be of the greatest possible service in improving egg production in farm and commercial flocks throughout the country.

8. Since most farmers are not in a position to carry on pedigree breeding work and since the average farm flock is composed of relatively poor producers, explain how the average farmer can best improve the laying qualities of his flock.

9. What are the most important effects that have been observed in cross-breeding poultry?

10. Explain what is meant by progeny testing, and tell why a pedigree poultry breeder should practice progeny testing regardless of whether he is breeding poultry primarily for show purposes or for egg production.

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APPENDIX

AGRICULTURAL COLLEGES AND EXPERIMENTAL STATION

Much of the material in this book is based upon the results of research carrie on at the various state experiment stations and other public institutions, especiall in the United States and Canada. Since it is highly probable that some reade of this book would like to write the institutions for further information alon certain lines, this list of institutions with their addresses has been prepared. Excep where noted, the state experiment stations in the United States are at the college of agriculture.

United States

Alabama: College of Agriculture, Auburn.
Arizona: College of Agriculture, Tucson.
Arkansas: College of Agriculture, Fayetteville.
California: College of Agriculture, Berkeley.
Colorado: College of Agriculture, Fort Collins.
Connecticut: College of Agriculture, Storrs.
Delaware: College of Agriculture, Newark.
Florida: College of Agriculture, Gainesville.
Georgia: College of Agriculture, Athens.
Idaho: College of Agriculture, Moscow.
Illinois: College of Agriculture, Urbana.
Indiana: College of Agriculture, Lafayette.
Iowa: College of Agriculture, Ames.
Kansas: College of Agriculture, Manhattan.
Kentucky: College of Agriculture, Lexington.
Louisiana: College of Agriculture, Baton Rouge.
Maine: College of Agriculture, Orono.
Maryland: College of Agriculture, College Park.
Massachusetts: College of Agriculture, Amherst.
Michigan: College of Agriculture, East Lansing.
Minnesota: College of Agriculture, St. Paul.
Mississippi: College of Agriculture, State College.
Missouri: College of Agriculture, Columbia.
Missouri: Poultry Experiment Station, Mountain Grove.
Montana: College of Agriculture, Bozeman.
Nebraska: College of Agriculture, Lincoln.
Nevada: College of Agriculture, Reno.
New Hampshire: College of Agriculture, Durham.
New Jersey: College of Agriculture, New Brunswick.
New Mexico: College of Agriculture, State College.
New York: College of Agriculture, Ithaca.
North Carolina: College of Agriculture, Raleigh.

North Dakota: College of Agriculture, Fargo.
Ohio: College of Agriculture, Columbus.
Ohio: Experiment Station, Wooster.
Oklahoma: College of Agriculture, Stillwater.
Oregon: College of Agriculture, Corvallis.
Pennsylvania: College of Agriculture, State College.
Rhode Island: College of Agriculture, Kingston.
South Carolina: College of Agriculture, Clemson.
South Dakota: College of Agriculture, Brookings.
Tennessee: College of Agriculture, Knoxville.
Texas: College of Agriculture, College Station.
Utah: College of Agriculture, Logan.
Vermont: College of Agriculture, Burlington.
Virginia: College of Agriculture, Blacksburg.
Washington: College of Agriculture, Pullman.
Washington: Western Washington Experiment Station, Puyallup.
West Virginia: College of Agriculture, Morgantown.
Wisconsin: College of Agriculture, Madison.
Wyoming: College of Agriculture, Laramie.

United States Department of Agriculture, Washington, D. C.
National Agricultural Research Center, Beltsville, Maryland.

Canada

Alberta: College of Agriculture, Edmonton.
British Columbia: College of Agriculture, Vancouver.
Manitoba: College of Agriculture, Winnipeg.
Nova Scotia: College of Agriculture, Truro.
Ontario: College of Agriculture, Guelph.
Quebec: Macdonald College.
Saskatchewan: College of Agriculture, Saskatoon.
Dominion Department of Agriculture, Ottawa.

TECHNICAL JOURNALS AND ABSTRACT REVIEWS

The literature references cited at the end of each chapter indicate the technical journals in which the various articles were published. The following is a list of the more important journals in which technical articles on poultry breeding and related topics are published or reviewed:

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American Veterinary Medical Association Journal, Chicago.
Anatomical Record, Philadelphia.
Archiv für Geflügelkunde, Berlin.
Biological Abstracts, Philadelphia.
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Canadian Journal of Research, Ottawa.
Endocrinology, Los Angeles.
Experiment Station Record, U. S. D. A., Washington, D. C.
Genetics, Brooklyn, N. Y.

Hereditas; Genetiski Arkiv, Lund.
Hilgardia, Berkeley, Cal.
International Review of Poultry Science, Rotterdam.
Journal of Agricultural Research, Washington, D. C.
Journal of Experimental Biology, New York.
Journal of Experimental Zoology, Philadelphia.
Journal of General Physiology, New York.
Journal of Genetics, London.
Journal of Heredity, Washington, D. C.
Physiological Reviews, Baltimore.
Poultry Science, Ithaca, N. Y.
Revue Française d'Endocrinologie, Paris.
Royal Society of Edinburgh, Proceedings.
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